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Language as shaped by the brain

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Abstract: It is widely assumed that human learning and the structure of human languages are intimately related. This relationship is frequently suggested to derive from a language-specific biological endowment, which encodes universal, but communicatively arbitrary, principles of language structure (a Universal Grammar or UG). How might such a UG have evolved? We argue that UG could not have arisen either by biological adaptation or non-adaptationist genetic processes, resulting in a *logical problem of language evolution*. Specifically, as the processes of language change are much more rapid than processes of genetic change, language constitutes a "moving target" both over time and across different human populations, and, hence, cannot provide a stable environment to which language genes could have adapted. We conclude that a biologically determined UG is not evolutionarily viable. Instead, the original motivation for UG – the mesh between learners and languages – arises because language has been shaped to fit the human brain, rather than vice versa. Following Darwin, we view language itself as a complex and interdependent "organism," which evolves under selectional pressures from human learning and processing mechanisms. That is, languages themselves are shaped by severe selectional pressure from each generation of language users and learners. This suggests that apparently arbitrary aspects of linguistic structure may result from general learning and processing biases deriving from the structure of thought processes, perceptuo-motor factors, cognitive limitations, and pragmatics.

Keywords: biological adaptation; cultural evolution; grammaticalization; language acquisition; language evolution; linguistic change; natural selection; Universal Grammar

1. Introduction

Natural language constitutes one of the most complex aspects of human cognition, yet children already have a good grasp of their native language before they can tie their shoes or ride a bicycle. The relative ease of acquisition suggests that when a child makes a "guess" about the structure of language on the basis of apparently limited evidence, the child has an uncanny tendency to guess right. This strongly suggests that there must be a close relationship between the mechanisms by which the child acquires and processes language and the structure of language itself.

What is the origin of this presumed close relationship between the mechanisms children use in acquisition and the structure of language? One view is that specialized brain mechanisms specific to language acquisition have evolved over long periods of natural selection (e.g., Pinker & Bloom 1990). A second view rejects the idea that these specialized brain mechanisms have arisen through adaptation, and assumes that they have emerged through some non-adaptationist route, just as it has been argued that many biological structures are not the product of adaptation (e.g., Bickerton 1995; Gould 1993; Jenkins 2000; Lightfoot 2000). Both these viewpoints put the explanatory emphasis on brain mechanisms specialized for language – and ask how they have evolved.

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In this target article, we develop and argue for a third view, which takes the opposite starting point: Our question is not, "Why is the brain so well suited to learning language?" Instead, we ask "Why is language so well suited to being learned by the brain?" We propose that *language* has adapted through gradual processes of cultural evolution to be easy to learn to produce and understand. Thus, the structure of human language must inevitably be shaped around human learning and processing biases deriving from the structure of our thought processes, perceptuo-motor factors, cognitive limitations, and pragmatic constraints. Language is easy for us to learn and use, not because our brains embody knowledge of language, but because language has adapted to our brains. Following Darwin (1874), we argue that it is useful metaphorically to view languages as "organisms" – that is, highly complex systems of interconnected constraints – that have evolved in a symbiotic relationship with humans. According to this view, whatever domain-general learning and processing biases people happen to have will tend to become embedded in the structure of language – because it will be easier to learn to understand and produce languages, or specific linguistic forms, that fit these biases.

We start by introducing "The Logical Problem of Language Evolution" (sect. 2), which faces theories proposing that humans have evolved specialized brain mechanisms for language. The following two sections, "Evolution of Universal Grammar by Biological Adaptation" (sect. 3) and "Evolution of Universal Grammar by Non-adaptationist Means" (sect. 4), evaluate adaptationist and non-adaptationist explanations of language evolution, concluding that both face insurmountable theoretical obstacles. Instead, we present an alternative perspective, "Language as Shaped by the Brain" (sect. 5), in which language is treated as an evolutionary system in its own right, adapting to the human brain. The next two sections, "Constraints on Language Structure" (sect. 6) and "How Constraints Shape Language over Time" (sect. 7), discuss what biases have shaped language evolution and how these can be observed in language change mediated by cultural transmission. Finally, in section 8, the "Scope of the Argument," we consider the wider implications of our theory of language evolution, including a radical recasting of the problem of language acquisition.

2. The logical problem of language evolution

For a period spanning three decades, Chomsky (1965; 1972; 1980; 1986; 1988; 1993) has argued that a substantial innate endowment of language-specific knowledge is necessary for language acquisition. These constraints form a *Universal Grammar* (UG); that is, a collection of grammatical principles that hold across all human languages. In this framework, a child's language ability gradually unfolds according to a genetic blueprint in much the same way as a chicken grows a wing (Chomsky 1988). The staunchest proponents of this view even go as far as to claim that "doubting that there are language-specific, innate computational capacities today is a bit like being still dubious about the very existence of molecules, in spite of the awesome progress of molecular biology" (Piattelli-Palmarini 1994, p. 335).

There is considerable variation in current conceptions of the exact nature of UG, ranging from being close to the Principle and Parameter Theory (PPT; Chomsky 1981) of pre-minimalist generative grammar (e.g., Crain & Pietroski 2006; Crain et al. 2006), to the Simpler Syntax (SS) version of generative grammar proposed by Jackendoff (2002) and colleagues (Culicover & Jackendoff 2005; Pinker & Jackendoff 2005), to the Minimalist Program (MP) in which language acquisition is confined to learning a lexicon from which cross-linguistic variation is proposed to arise (Boeckx 2006; Chomsky 1995). From the viewpoint of PPT, UG consists of a set of genetically specified universal linguistic principles combined with a set of parameters to account for variations among languages (Crain et al. 2006). Information from the language environment is used during acquisition to determine the parameter settings relevant for individual languages. The SS approach combines elements from construction grammar (e.g., Goldberg 2006) with more traditional structural principles from generative grammar, including principles relating to phrase structure (X-bar theory), agreement, and case-marking. Along with constraints arising from the syntax-semantic interface, these basic structural principles form part of a universal "toolkit" of language-specific mechanisms, encoded in a genetically specified UG (Culicover & Jackendoff 2005). By contrast, proponents of MP construe language as a perfect system for mapping between sound and meaning (Chomsky 1995). In departure from earlier generative approaches, only recursion (in the form of Merge) is considered to be unique to the human language ability (Hauser et al. 2002). Variation among languages is now explained in terms of lexical parameterization (Borer 1984); that is, differences between languages are no longer explained in terms of parameters associated with grammars (as in PPT), but primarily in terms of parameters associated with particular lexical items (though some non-lexical parameters currently remain; Baker 2001; Boeckx 2006).

Common to these three current approaches to generative grammar is the central assumption that the constraints of UG (whatever their form) are fundamentally arbitrary – that is, not determined by functional considerations. That is, these principles cannot be explained in terms of learning, cognitive constraints, or communicative effectiveness. For example, consider the principles of binding, which have come to play a key role in generative linguistics (Chomsky 1981). The principles of binding capture patterns of, among other things, reflexive pronouns (e.g., *himself*, *themselves*) and accusative pronouns (*him*, *them*, etc.), which appear, at first sight, to defy functional explanation. Consider Examples (1) to (4), where the subscripts indicate co-reference, and asterisks indicate ungrammaticality.

1. John$_i$ sees himself$_i$.
2. *John$_i$ sees him$_i$.
3. John$_i$ said he$_{i/j}$ won.
4. *He$_i$ said John$_i$ won.

In (1) the pronoun *himself* must refer to John; in (2) it cannot. In (3) the pronoun *he* may refer to John or to another person; in (4) it cannot refer to John. These and many other cases indicate that an extremely rich set of patterns govern the behavior of pronouns, and these patterns appear arbitrary – it appears that numerous alternative patterns would, from a functional standpoint, serve

equally well. These patterns are instantiated in PPT by the principles of binding theory (Chomsky 1981), in SS by constraints arising from structural and/or syntax-semantics interface principles (Culicover & Jackendoff 2005), and in MP by limitations on movement (internal merge; Hornstein 2001). Independent of their specific formulations, the constraints on binding, while apparently universal across natural languages, are assumed to be arbitrary and, hence, may be presumed to be part of the genetically encoded UG.

Putative arbitrary universals, such as the restrictions on binding, contrast with functional constraints on language. Whereas the former are hypothesized to derive from the internal workings of a UG-based language system, the latter originate from cognitive and pragmatic constraints related to language acquisition and use. Consider the tendency in English to place long phrases after short ones; for example, as evidenced by so-called "heavy-NP shifts." In Example (5) shown below, the long (or "heavy") direct-object noun phrase (NP), *the book he had not been able to locate for over two months*, appears at the end of the sentence, separated from its canonical postverbal position by the prepositional phrase (PP) *under his bed*. Both corpus analyses (Hawkins 1994) and psycholinguistic sentence-production experiments (Stallings et al. 1998) suggest that Example (5) is much more acceptable than the standard (or "non-shifted") version in Example (6), in which the direct-object NP is placed immediately following the verb.

5. John found $_{PP}$[under his bed] $_{NP}$[the book he had not been able to locate for over two months].

6. John found $_{NP}$[the book he had not been able to locate for over two months] $_{PP}$[under his bed].

Whereas individuals speaking head-initial languages, such as English, tend to prefer short phrases before long ones, speakers of head-final languages, such as Japanese, have been shown to have the opposite long-before-short preference (Yamashita & Chang 2001). In both cases, the preferential ordering of long versus short phrases can be explained in terms of minimization of memory load and maximization of processing efficiency (Hawkins 2004). As such, the patterns of length-induced phrasal reordering are generally considered within generative grammar to be a performance issue related to functional constraints outside the purview of UG (although some functionally oriented linguists have suggested that these kinds of performance constraints may shape grammar itself; e.g., Hawkins 1994; 2004). In contrast, the constraints inherent in UG are arbitrary and non-functional in the sense that they do not relate to communicative or pragmatic considerations, nor do they derive from limitations on the mechanisms involved in using or acquiring language. Indeed, some generative linguists have argued that aspects of UG hinder communication (e.g., Chomsky 2005b; Lightfoot 2000).

If we suppose that such arbitrary principles of UG are genetically specified, then this raises the question of the evolutionary origin of this genetic endowment. Two views have been proposed. *Adaptationists* emphasize a gradual evolution of the human language faculty through *natural selection* (e.g., Briscoe 2003; Corballis 1992; 2003; Dunbar 2003; Greenfield 1991; Hurford 1991; Jackendoff 2002; Nowak et al. 2001; Pinker 1994; 2003; Pinker & Bloom 1990; Pinker & Jackendoff 2005). Linguistic ability confers added reproductive fitness, leading to a selective pressure for language genes[1]; richer language genes encode increasingly elaborate grammars. In contrast, *non-adaptationists* (e.g., Bickerton 1995 – but see Bickerton 2003; Chomsky 1988; Jenkins 2000; Lightfoot 2000; Piattelli-Palmarini 1989) suggest that natural selection played only a minor role in the emergence of language in humans, focusing instead on a variety of alternative possible evolutionary mechanisms by which UG could have emerged de novo (e.g., as a result of as few as two or three key mutation "events"; Lanyon 2006).

In the next two sections, 3 and 4, we argue that both of these views, as currently formulated, face profound theoretical difficulties resulting in a *logical problem of language evolution*.[2] This is because, on analysis, it is mysterious how proto-language – which must have been, at least initially, a cultural product likely to be highly variable over both time and geographical locations – could have become genetically fixed as a highly elaborate biological structure. Hence, there is no currently viable account of how a genetically encoded UG could have evolved. In subsequent sections (5 to 7), we argue that the brain does not encode principles of UG – and therefore neither adaptationist nor non-adaptationist solutions are required. Instead, language has been shaped by the brain: Language reflects pre-existing, and hence non-language-specific, human learning and processing mechanisms.

3. Evolution of Universal Grammar by biological adaptation

The adaptationist position is probably the most widely held view of the origin of UG. We first describe adaptationism in biology and its proposed application to UG before outlining three conceptual difficulties for adaptationist explanations of language evolution.

3.1. Adaptation: The very idea

Adaptation is a candidate explanation for the origin of any innate biological structure. In general, the idea is that natural selection has favored genes that code for biological structures that increase *fitness* (in terms of expected numbers of viable offspring).[3] Typically, a biological structure contributes to fitness by fulfilling some purpose – the heart is assumed to pump blood, the legs to provide locomotion, or UG to support language acquisition. If so, natural selection will generally favor biological structures that fulfill their purpose well, so that, over the generations, hearts will become well adapted to pumping blood, legs well adapted to locomotion, and any presumed biological endowment for language acquisition will become well adapted to acquiring language.

Perhaps the most influential statement of the adaptationist viewpoint is by Pinker and Bloom (1990). They argue that "*natural selection is the only scientific explanation of adaptive complexity*. 'Adaptive complexity' describes any system composed of many interacting parts where the details of the parts' structure and arrangement suggest design to fulfill some function" (p. 709; their emphasis). As another example of adaptive complexity, they refer to the exquisite optical and computational sophistication of the vertebrate visual system. Pinker and Bloom note that such a complex and intricate mechanism

has an extremely low probability of occurring by chance. Whatever the influence of non-adaptational factors (see sect. 4 of our article), they argue that there must additionally have been substantial adaptation to fine-tune a system as complex as the visual system. Given that language appears as complex as vision, Pinker and Bloom conclude that it is also highly improbable that language is entirely the product of non-adaptationist processes (see also Pinker 2003).

The scope and validity of the adaptationist viewpoint in biology is controversial (e.g., Dawkins 1986; Gould 2002; Gould & Lewontin 1979; Hecht Orzak & Sober 2001); and some theorists have used this controversy to question adaptationist views of the origin of UG (e.g., Bickerton 1995; Lewontin 1998). Here, we take a different tack. We argue that, whatever the merits of adaptationist explanation in general, and as applied to vision in particular, the adaptationist account cannot extend to a putative UG.

3.2. Why Universal Grammar could not be an adaptation to language

Let us suppose that a genetic encoding of universal properties of language did, as the adaptationist view holds, arise as an adaptation to the environment, here to the *linguistic* environment. This point of view seems to work most naturally for aspects of language that have a transparent *functional* value. For example, the compositional character of language (i.e., the ability to express in an infinite number of messages using a finite number of lexical items) seems to have great functional advantages. A biological endowment that allows, or perhaps requires, that language has this form appears likely to lead to enhanced communication; and hence, to be positively selected. Thus, over time, functional aspects of language might be expected to become genetically encoded across the entire population. But UG, according to Chomsky (e.g., 1980; 1988), consists precisely of linguistic principles that appear highly abstract and arbitrary – that is, they have no functional significance. To what extent can an adaptationist account of the evolution of a biological basis for language explain how a genetic basis could arise for such abstract and arbitrary properties of language?

Pinker and Bloom (1990) provide an elegant approach to this question. They suggest that the constraints imposed by UG, such as the binding constraints (mentioned in sect. 2 above), can be construed as communication protocols for transmitting information over a serial channel. Although the general features of such protocols (e.g., concerning compositionality, or the use of a small set of discrete symbols) may be functionally important, many of the specific aspects of the protocol do not matter, as long as everyone (within a given speech community) adopts the *same* protocol. For example, when using a modem to communicate between computers, a particular protocol might have features such as odd parity, handshake on, 7 bit, and so forth. However, there are many other settings that would be just as effective. What is important is that the computers that are to interact adopt the *same* set of settings – otherwise communication will not be possible. Adopting the same settings is therefore of fundamental functional importance to communication between computers, but the particular choice of settings is not. Similarly, when it comes to the specific features of UG, Pinker and Bloom suggest that "in the evolution of the language faculty, many 'arbitrary' constraints may have been selected simply because they defined parts of a standardized communicative code in the brains of some critical mass of speakers" (1990, p. 718).[4] Thus, such arbitrary constraints on language can come to have crucial adaptive value to the language user; genes that favor such constraints will be positively selected. Over many generations, the arbitrary constraints may then become innately specified.

We will argue that this viewpoint faces three fundamental difficulties, concerning the dispersion of human populations, language change, and the question of *what* is genetically encoded. We consider these in turn.

3.2.1. Problem 1: The dispersion of human populations. Pinker and Bloom's (1990) analogy with communications protocols, while apt, is, however, something of a double-edged sword. Communications protocols and other technical standards typically diverge rapidly unless there is concerted oversight and enforcement to maintain common standards. Maintaining and developing common standards is an integral part of software and hardware development. In the absence of such pressures for standardization, protocols would rapidly diverge. Given that language presumably evolved without top-down pressures for standardization, divergence between languages seems inevitable. To assume that "universal" arbitrary features of language would emerge from adaptation by separate groups of language users, would be analogous to assuming that the same set of specific features for computer communication protocols might emerge from separate teams of scientists, working in separate laboratories (e.g., that different modem designers independently alight on odd parity, handshake on, 7-bit error correction, and so on). Note that this point would apply equally well, even if the teams of scientists emerged from a single group. Once cut off from each other, groups would develop in independent ways.

Indeed, in biological adaptation, genes appear to rapidly evolve to deal with a specific local environment. Thus, Darwin observed rich patterns of variations in fauna (e.g., finches) across the Galapagos Islands, and interpreted these variations as adaptation to local island conditions. Hence, if language genes have adapted to local linguistic environments, we should expect a range of different biologically encoded UGs, each specifically adapted to its local linguistic context. Indeed, one might expect, if anything, that language-genes would diverge especially rapidly – because the linguistic environment in each population is assumed to be itself shaped by the different language-genes in each subpopulation, thus amplifying the differences in the linguistic environment. If so, then people should have, at minimum, some specific predisposition to learn and process languages associated with their genetic lineage. This does not appear to be the case, and it is a key assumption of the generative linguistics perspective that the human language endowment does not vary in this way but is universal across the species (Chomsky 1980; Pinker 1994).

There is an interesting contrast here with the human immune system, which has evolved to a very rapidly changing microbial environment. Crucially, the immune system can build new antibody proteins (and the genetic mechanisms from which antibody proteins are constructed)

without having to eliminate old antibody proteins (Goldsby et al. 2003). Therefore, natural selection will operate to *enrich* the coverage of the immune system (though such progress will not always be cumulative, of course); there is no penalty for the immune system following a fast-moving "target" (defined by the microbial environment). But the case of acquiring genes coding for regularities in language is very different – because, at any one time, there is just one language (or at most two or three) that must be acquired – and, hence, a bias that helps learn a language with property *P* will thereby *inhibit* learning languages with not-*P*. The fact that language change is so fast (so that whether the current linguistic environment has property *P* or not will vary rapidly, in the time-scale of biological evolution) means that such biases will, on balance, be counterproductive.

Given that the immune system does co-evolve with the microbial environment, different co-evolutionary paths have been followed when human populations have diverged. Therefore, populations that have co-evolved to their local microbial environment are often poorly adapted to other microbial environments. For example, when Europeans began to explore the New World, they succumbed in large numbers to the diseases they encountered, while conversely, European diseases caused catastrophic collapse in indigenous populations (e.g., Diamond 1997). If an innate UG had co-evolved with the linguistic environment, similar radically divergent co-evolutionary paths might be expected. Yet, as we have noted, the contrary appears to be the case.

The problem of divergent populations arises across a range of different scenarios concerning the relationship between language evolution and the dispersion of human populations. One scenario is that language evolution is recent and occurred during the dispersion of modern humans (*Homo sapiens sapiens*). In this case, whether language was discovered once, and then spread throughout human populations, or was discovered in various locations independently, there remains the problem that adaptations to language would not be coordinated across geographically dispersed groups. It is tempting to suggest that all of these sublanguages will, nonetheless, obey universal grammatical principles, thus providing some constancy in the linguistic environment. But this appeal would, of course, be circular, as we are attempting to explain the *origin* of such principles. We shall repeatedly have to steer around this *circularity trap* below.

An alternative scenario is that language evolution predates the dispersion of modern humans. If so, then it is conceivable that prior dispersions of hominid populations, perhaps within Africa, did lead to the emergence of diverse languages and diverse UGs, adapted to learning and processing such languages, and therefore that, subsequently, one local population proved to be adaptively most successful and came to displace other hominid populations. Thus, on this account, our current UG might conceivably be the only survivor of a larger family of such UGs as a result of a population "bottleneck" – the universality of UG would arise, then, because it was genetically encoded in the sub-population from which modern humans descended.[5]

This viewpoint is not without difficulties. Some interpretations of the genetic and archaeological evidence suggest that the last bottleneck in human evolution occurred at between 500,000 and 2,000,000 years ago (e.g., Hawks et al. 2000); few researchers in language evolution believe that language, in anything like its modern form, is this old. Moreover, even if we assume a more recent bottleneck, any such bottleneck must at least predate the 100,000 years or so since the geographical dispersion of human populations, and 100,000 years still seems to provide sufficient time for substantial linguistic divergence to occur. Given that the processes of genetic adaptation to language most likely would continue to operate,[6] different genetic bases for language would be expected to evolve across geographically separated populations. That is, the evolution of UG by adaptation would appear to require rapid adaptations for language prior to the dispersion of human populations, followed by an abrupt cessation of such adaptation, for a long period after dispersion. The contrast between the evolution of the putative "language organ" and that of biological processes, such as digestion, is striking. The digestive system is evolutionarily very old, and many orders of magnitude older than the recent divergence of human populations. Nonetheless, digestion appears to have adapted in important ways to recent changes in the dietary environment; for example, with apparent co-evolution of lactose tolerance and the domestication of milk-producing animals (Beja-Pereira et al. 2003).

3.2.2. Problem 2: Language change. Whatever the timing of the origin of language and hominid dispersion, the thesis that a genetically encoded UG arose through adaptation faces a second problem: that, even within a single population, linguistic conventions change rapidly. Hence, the linguistic environment over which selectional pressures operate presents a "moving target" for natural selection. If linguistic conventions change more rapidly than genes change via natural selection, then genes that encode biases for particular conventions will be eliminated – because, as the language changes, the biases will be incorrect, and, hence, decrease fitness. More generally, in a fast-changing environment, phenotypic flexibility to deal with various environments will typically be favored over genes that bias the phenotype narrowly toward a particular environment. Again, there is a tempting counterargument – that the linguistic principles of UG will *not* change, and hence these aspects of language will provide a stable linguistic environment over which adaptation can operate. But, of course, this argument falls into the circularity trap, because the genetic endowment of UG is proposed to *explain* language universals; so it cannot be assumed that the language universals pre-date the emergence of the genetic basis for UG.

Christiansen et al. (2006) illustrate the problems raised by language change in a series of computer simulations. They assume the simplest possible set-up: that (binary) linguistic principles and language "genes" stand in a one-to-one correspondence. Each gene has three alleles – two, each of which is biased in favor of a version of the corresponding principle, and one neutral allele.[7] Agents learn the language by trial-and-error, where their guesses are biased according to which alleles they have. The fittest agents are allowed to reproduce, and a new generation of agents is produced by sexual recombination and mutation. When the language is fixed, there is a selection pressure in favor of the "correctly" biased genes, and these rapidly come to dominate the population, as illustrated by Figure 1. This is an instance of the *Baldwin effect*

(Baldwin 1896; for discussion, see Weber & Depew 2003) in which information that is initially learned becomes encoded in the genome.

A frequently cited example of the Baldwin effect is the development of calluses on the keels and sterna of ostriches (Waddington 1942). The proposal is that calluses are initially developed in response to abrasion where the keel and sterna touch the ground during sitting. Natural selection then favored individuals that could develop calluses more rapidly, until callus development became triggered within the embryo and could occur without environmental stimulation. Pinker and Bloom (1990) suggest that the Baldwin effect in a similar way could be the driving force behind the adaptation of UG. Natural selection will favor learners who are genetically disposed rapidly to acquire the language to which they are exposed. Hence, over many generations this process will lead to a genetically specified UG.

However, when language is allowed to change (e.g., because of exogenous forces such as language contact), the effect reverses – biased genes are severely selected against when they are inconsistent with the linguistic environment, and neutral genes come to dominate the population. The selection in favor of neutral genes occurs even for low levels of language change (i.e., the effect occurs, to some degree, even if language change equals the rate of genetic mutation). But, of course, linguistic change (prior to any genetic encoding) is likely to have been much faster than genetic change. After all, in the modern era, language change has been astonishingly rapid, leading, for example, to the wide phonological and syntactic diversity of the Indo-European language group, from a common ancestor about 10,000 years ago (Gray & Atkinson 2003). Language in hunter-gatherer societies changes at least as rapidly. Papua, New Guinea, settled within the last 50,000 years, has an estimated one-quarter of the world's languages. These are enormously linguistically diverse, and most originate in hunter-gatherer communities (Diamond 1992).[8]

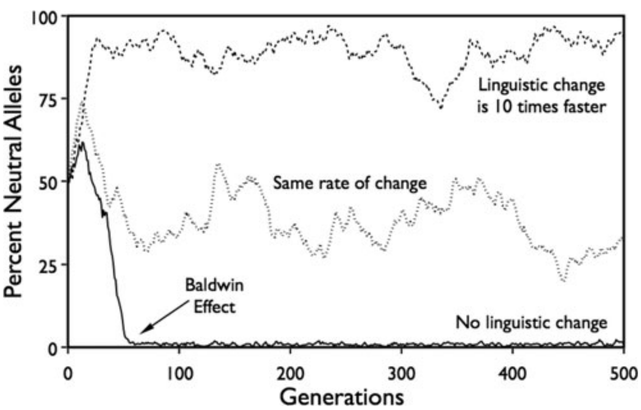


Figure 1. *The effect of linguistic change on the genetic encoding of arbitrary linguistic principles.* Results are shown from a simulation with a population size of 100 agents, a genome size of 20, survival of the top 50% of the population, and starting with 50% neutral alleles. When there is no linguistic change, alleles encoding specific aspects of language emerge quickly – that is, a Baldwin effect occurs – but when language is allowed to change, neutral alleles become more advantageous. Similar results were obtained across a wide range of different simulation parameters. (Adapted from Christiansen, Reali & Chater 2006)

Thus, from the point of view of natural selection, it appears that language, like other cultural adaptations, changes far too rapidly to provide a stable target over which natural selection can operate. Human language learning, therefore, may be analogous to typical biological responses to high levels of environmental change – that is, to develop general-purpose strategies which apply across rapidly changing environments, rather than specializing to any particular environment. This strategy appears to have been used, in biology, by "generalists" such as cockroaches and rats, in contrast, for example, to pandas and koalas, which are adapted to extremely narrow environmental niches.

A potential limitation of our argument so far is that we have assumed that changes in the linguistic environment are "exogenous." But many aspects of language change may be "endogenous," that is, may arise because the language is adapting as a result of selection pressures from learners, and, hence, their genes. Thus, one might imagine the following argument: Suppose there is a slight, random, genetic preference for languages with feature *A* rather than *B*. Then this may influence the language spoken by the population to have feature *A*, and this may in turn select for genes that favor the feature *A*.[9] Such feedback might, in principle, serve to amplify small random differences into, ultimately, rigid arbitrary language universals. However, as Figure 2 illustrates, when linguistic change is genetically influenced, rather than random, it turns out that, while this amplification effect can occur, and lead to a Baldwin effect, it does not emerge from small random fluctuations. Instead, it only occurs when language is initially strongly influenced by genes. But if arbitrary features of language would have to be predetermined strongly by the genes from the very beginning, then this leaves little scope for subsequent operation of the Baldwin effect as envisioned by Pinker and Bloom (1990).

3.2.3. Problem 3: What is genetically encoded? Even if the first two difficulties for adaptationist accounts of UG could be solved, the view still faces a further puzzle:

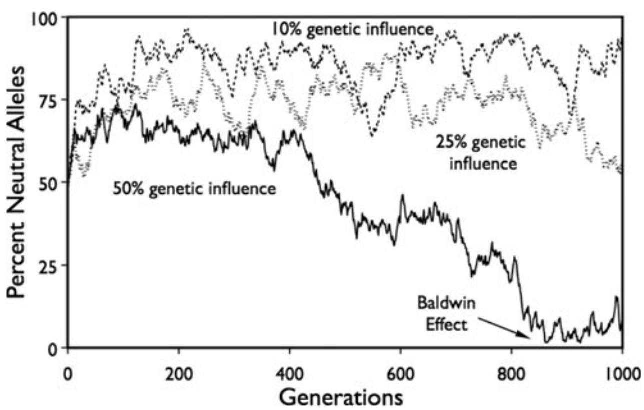


Figure 2. *The Baldwin effect*, where genes influence language: the role of population influence (i.e., genetic "feedback") on the emergence of the Baldwin effect for language-relevant alleles when language is allowed to change 10 times faster than biological change. Only when the pressure from the learners' genetic biases is very high ($\sim 50\%$) can the Baldwin effect overcome linguistic change. (Adapted from Christiansen, Reali & Chater 2006)

Why is it that genetic adaptation occurred only to very abstract properties of language, rather than also occurring to its superficial properties? Given the spectacular variety of surface forms of the world's languages, in both syntax (including every combination of basic orderings of subject, verb and object, and a wide variety of less constrained word orders) and phonology (including tone and click languages, for example), why did language genes not adapt to these surface features?[10] Why should genes become adapted to capture the extremely rich and abstract set of possibilities countenanced by the principles of UG, rather than merely encoding the actual linguistic possibilities in the specific language that was being spoken (i.e., the phonological inventory and particular morphosyntactic regularities of the early click-language, from which the Khoisan family originated and which might be the first human language; e.g., Pennisi 2004)? The unrelenting abstractness of the universal principles makes them difficult to reconcile with an adaptationist account.

One of the general features of biological adaptation is that it is driven by the constraints of the immediate environment. It can have no regard for distant or future environments that might one day be encountered. For example, the visual system is highly adapted to the laws of optics as they hold in normal environments. Thus, the length of a stick in water is misestimated by human vision, because it does not correct for the refraction of light through water (this being not commonly encountered in the human visual world). By contrast, the visual system of the archerfish, which must strike airborne flies with a water jet from below the water surface, does make this correction (Rossel et al. 2002). Biological adaptation produces systems designed to fit the environment to which adaptation occurs; there is, of course, no selectional pressure to fit environments that have not occurred or those that might occur at some point in the future. Hence, if a UG did adapt to a past linguistic environment, it would seem inevitable that it would adapt to that language environment *as a whole*: thus adapting to its *specific* word order, phonotactic rules, inventory of phonemic distinctions, and so on. In particular, it seems very implausible that an emerging UG would be selected primarily for extremely abstract features, which apply equally to all possible human languages, not just the language evident in the linguistic environment in which selection operates. This would be analogous to an animal living in a desert environment somehow developing adaptations that are not specific to desert conditions, but that are equally adaptive in all terrestrial environments.

The remarkable abilities of the young indigo bunting to use stars for navigational purposes – even in the absence of older birds to lead the way – might at first seem to counter this line of reasoning (e.g., Hauser 2001; Marcus 2004). Every autumn this migratory bird uses the location of Polaris in the night sky to fly from its summer quarters in the Northeast United States to its winter residence in the Bahamas. As demonstrated by Emlen (1970), the indigo bunting uses celestial rotation as a reference axis to discover which stars point to true north. Thus, when Emlen raised young fledglings in a planetarium that was modified to rotate the night sky around Betelgeuse, the birds oriented themselves as if north was in the direction of this bright star. Crucially, what has become genetically encoded is not a star map – because star constellations change over evolutionary time and thus form moving targets – but instead that which is stable: that stationary stars indicate the axis of earth's rotation, and hence true north.

Similarly, it is tempting to claim that the principles of UG are just those that are invariant across languages, whereas contingent aspects of word order or phonology will vary across languages. Thus, one might suggest that only the highly abstract, language-universal, principles of UG will provide a stable basis upon which natural selection can operate. But this argument is again, of course, a further instance of the circularity trap. We are trying to explain how a putative UG might become genetically fixed, and hence we cannot assume UG is already in place. Thus, this counterargument is blocked.

We are not, of course, arguing that abstract structures cannot arise by adaptation. Indeed, abstract patterns, such as the body plan of mammals or birds, are conserved across species and constitute a complex and highly integrated system. Notice, though, that such abstract structures are still tailored to the specific environment of each species. Thus, while bats, whales, and cows have a common abstract body plan, these species embody dramatically different instantiations of this pattern, adapted to their ecological niches in the air, in water, or on land. Substantial modifications of this kind can occur quite rapidly, as a result of changes in a small numbers of genes and/or their pattern of expression. For example, the differing beak shape in Darwin's finches, adapted to different habitats in the Galapagos Islands, may be largely determined by as few as two genes: *BMP4*, the expression of which is associated with the width, as well as depth, of beaks (Abzhanov et al. 2004), and *CaM*, the expression of which is correlated with beak length (Abzhanov et al. 2006). Again, these adaptations are all related closely to the local environment in which an organism exists. In contrast, adaptations for UG are hypothesized to be for abstract principles holding across all linguistic environments, with no adaptation to the local environment of specific languages and language users.

In summary, Pinker and Bloom (1990), as we have seen, draw a parallel between the adaptationist account of the development of the visual system and an adaptationist account of a putative language faculty. But the above arguments indicate that the two cases are profoundly different. The principles of optics and the structure of the visual world have many invariant features across environments (e.g., Simoncelli & Olshausen 2001), but the linguistic environment is vastly different from one population to another. Moreover, the linguistic environment, unlike the visual environment, will itself be altered in line with any genetic changes in the propensity to learn and use languages, thus further amplifying differences between linguistic environments. We conclude, then, that linguistically driven biological adaptation cannot underlie the evolution of language.

It remains possible, though, that the development of language did have a substantial impact on biological evolution. The arguments given here merely preclude the possibility that linguistic conventions that would originally *differ* across different linguistic environments could somehow become universal across all linguistic communities, by virtue of biological adaptation to the linguistic environment. This is because, in the relevant respects, the linguistic environment for the different populations is highly variable, and hence any biological adaptations could only serve to entrench such differences further.

But there might be features that are universal across linguistic environments that might lead to biological adaptation, such as the means of producing speech (Lieberman 1984), or the need for enhanced memory capacity, or complex pragmatic inferences (Givón & Malle 2002). However, these language features are likely to be functional – that is, they facilitate language *use* – and therefore would typically not be considered part of UG.

It is consistent with our arguments that the emergence of language influenced biological evolution in a more indirect way. The possession of language might have fundamentally changed the patterns of collective problem solving and other social behavior in early humans, with a consequent shift in the selectional pressures on humans engaged in these new patterns of behavior. But universal, arbitrary constraints on the structure of language cannot emerge from biological adaptation to a varied pattern of linguistic environments. Thus, the adaptationist account of the biological origins of UG cannot succeed.

4. Evolution of Universal Grammar by non-adaptationist means

Some theorists advocating a genetically based UG might concur with our arguments against adaptationist accounts of language evolution. For instance, Chomsky (1972; 1988; 1993) has for more than two decades expressed strong doubts about neo-Darwinian explanations of language evolution, hinting that UG may be a by-product of increased brain size or yet unknown physical or biological evolutionary constraints. Further arguments for a radically non-adaptationist perspective have been advanced by Jenkins (2000), Lanyon (2006), Lightfoot (2000), and Piattelli-Palmarini (1989; 1994).

Non-adaptationists typically argue that UG is both highly complex and radically different from other biological machinery (though see Hauser et al. 2002). They suggest, moreover, that UG appears to be so unique in terms of structure and properties, that it is unlikely to be a product of natural selection amongst random mutations. However, we argue that non-adaptationist attempts to explain a putative language-specific genetic endowment also fail.

To what extent can any non-adaptationist mechanism account for the development of a genetically encoded UG, as traditionally conceived? In particular, can such mechanisms account for the appearance of genetically specified properties that are presumed to be (a) idiosyncratic to language, and (b) of substantial complexity? We argue that the probability that non-adaptationist factors played a substantial role in the evolution of UG is vanishingly small.

The argument involves a straightforward application of information theory. Suppose that the constraints embodied in UG are indeed language-specific and hence do not emerge as side-effects of existing processing mechanisms. This means that UG would have to be generated *at random* by non-adaptationist processes. Suppose further that the information required to specify a language acquisition device, so that language can be acquired and produced, over and above the pre-linguistic biological endowment can be represented as a binary string of N bits (this particular coding assumption is purely for convenience). Then the probability of generating this sequence of N bits by chance is 2^{-N}. If the language-specific information could be specified using a binary string that would fit on one page of normal text (which would presumably be a considerable underestimate, from the perspective of most linguistic theory), then N would be over 2,500. Hence, the probability of generating the grammar by a random process would be less than $2^{-2,500}$. So, to generate this machinery by chance (i.e., without the influence of the forces of adaptation) would be expected to require of the order of $2^{2,500}$ individuals. But the total population of humans over the last two million or so years, including the present, is measured in billions and is much smaller than 2^{35}. Hence, the probability of non-adaptationist mechanisms "chancing" upon a specification of a language organ or language instinct through purely non-adaptationist means is astronomically unlikely.[11]

It is sometimes suggested, apparently in the face of this type of argument, that the recent evolutionary–developmental biology literature has revealed how local genetic changes, for example, on homeobox genes, can influence the expression of other genes, and through a cascade of developmental influences, result in extensive phenotypic consequences (e.g., Gerhart & Kirschner 1997; Laubichler & Maienschein 2007). Yet, suppose that UG arises from a small "tweak" to pre-linguistic cognitive machinery; then general cognitive machinery will provide the vast bulk of the explanation of language structure. Without this machinery, the impact of the tweak would be impossible to understand. Thus, the vision of Universal Grammar as a language-specific innate faculty or language organ would have to be retracted. But the idea that a simple tweak might lead to a complex, highly interdependent, and intricately organized system, such as the putative UG, is highly implausible. Small genetic changes lead to modifications of existing complex systems, and these modifications can be quite far-reaching; however, they do not lead to the construction of new complexity. A mutation might lead to an insect having an extra pair of legs, and a complex set of genetic modifications (almost certainly over strong and continuous selectional pressure) may modify a leg into a flipper, but no single gene creates an entirely new means of locomotion, from scratch. The whole burden of the classic arguments for UG is that UG is both highly organized and complex, and utterly distinct from general cognitive principles. Thus, the emergence of a putative UG requires the construction of a new complex system, and the argument sketched above notes that the probability of even modest new complexity arising by chance is astronomically low.

The implication of this argument is that it is extremely unlikely that substantial quantities of linguistically idiosyncratic information have been specified by non-adaptationist means. Indeed, the point applies more generally to the generation of any complex, functional biological structures. Thus, it is not clear how any non-adaptationist account can explain the emergence of something as intricately complex as UG.

Some authors who express skepticism concerning the role of adaptation implicitly recognize this kind of theoretical difficulty. Instead, many apparently complex and arbitrary aspects of cognition and language are suggested to have emerged out of the constraints on building any complex information processing system, given perhaps currently unknown physical and biological constraints

(e.g., Chomsky 1993; see Kauffman [1995] for a related viewpoint on evolutionary processes). A related perspective is proposed by Gould (1993), who views language as a *spandrel* – that is, as emerging as a by-product of other cognitive processes. Another option would be to appeal to *exaptation* (Gould & Vrba 1982), whereby a biological structure that was originally adapted to serve one function is put to use to serve a novel function. Yet the non-adaptationist attracted by these or other non-adaptationist mechanisms is faced with a dilemma. If language can emerge from general physical, biological, or cognitive factors, then the complexity and idiosyncrasy of UG is illusory; language emerges from general non-linguistic factors, a conclusion entirely consistent with the view we advocate here. If, by contrast, UG is maintained to be sui generis and not readily derivable from general processes, the complexity argument bites: the probability of a new and highly complex adaptive system emerging by chance is astronomically low.

The dilemma is equally stark for the non-adaptationist who attempts to reach for other non-adaptationist mechanisms of evolutionary change. There are numerous mechanisms that amount to random perturbations (from the point of view of the construction of a highly complex adaptive system) (Schlosser & Wagner 2004). These include *genetic drift* (Suzuki et al. 1989), the random fluctuations in gene frequencies in a population; *genetic hitch-hiking* (Maynard-Smith 1978), a mechanism by which non-selected genes "catch a ride" with another gene (nearby on the chromosome) that was subject to selection; *epigenesis* (Jablonka & Lamb 1989), which causes heritable cell changes as a result of environmental influences but without corresponding changes to the basic DNA sequences of that cell; *horizontal genetic transfer* (Syvanen 1985) by which genetic material shifts from one species to another; and *transposons* (McClintock 1950), mobile genetic elements that can move around in different positions within the genome of a cell and thus alter its phenotype. Each of these mechanisms provides a richer picture of the mechanisms of evolutionary change, but none provides an answer to the question of how novel and highly complex adaptive systems, such as the putative UG, might emerge de novo. However, if language is viewed as embodying novel complexity, then the emergence of this complexity by non-adaptationist (and hence, from an adaptive point of view, random) mechanisms is astronomically unlikely.

We may seem to be faced with a paradox. It seems clear that the mechanisms involved in acquiring and processing language are enormously intricate and moreover intimately connected to the structure of natural languages. The complexity of these mechanisms rules out, as we have seen in this section, a non-adaptationist account of their origin. However, if these mechanisms arose through adaptation, this adaptation cannot, as we argued in section 3, have been adaptation *to language*. But if the mechanisms that currently underpin language acquisition and processing were originally adapted to carry out other functions, then how is their apparently intimate relationship with the structure of natural language to be explained? How, for example, are we to explain that the language acquisition mechanisms seem particularly well adapted to learning natural languages, but not to any of a vast range of conceivable non-natural languages (e.g., Chomsky 1980)? As we now argue, the paradox can be resolved if we assume that the "fit" between the mechanisms of language acquisition and processing, on the one hand, and natural language, on the other, has arisen because natural languages themselves have "evolved" to be as easy to learn and process as possible: Language has been shaped by the brain, rather than vice versa.

5. Language as shaped by the brain

We propose, then, to invert the perspective on language evolution, shifting the focus from the evolution of *language users* to the evolution of *languages*. Figure 3 provides a conceptual illustration of these two perspectives (see also Andersen 1973; Hurford 1990; Kirby & Hurford 1997). The UG adaptationists (a) suggest that selective pressure toward better language abilities gradually led to the selection of more sophisticated UGs. In contrast, (b) we propose to view language as an evolutionary system in its own right (see also e.g., Christiansen 1994; Deacon 1997; Keller 1994; Kirby 1999; Ritt 2004), subject to adaptive pressures from the human brain. As a result, linguistic adaptation allows for the evolution of increasingly expressive languages that can nonetheless still be learned and processed by domain-general mechanisms. From this perspective, we argue that the mystery of the fit between human language acquisition and processing mechanisms and natural language may be unraveled; and we might, furthermore, understand how language has attained its apparently "idiosyncratic" structure.

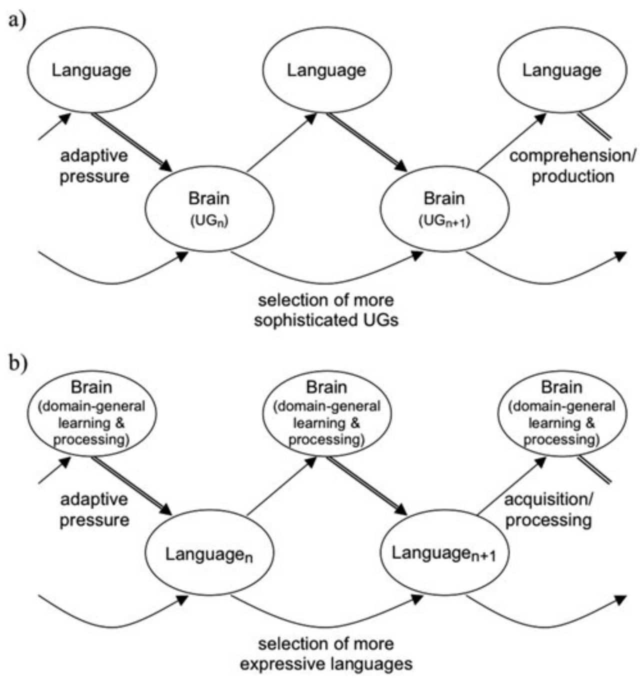


Figure 3. *Illustration of two different views on the direction of causation in language evolution:* (a) biological adaptations of the brain to language (double arrows), resulting in gradually more intricate UGs (curved arrows) to provide the basis for increasingly complex language production and comprehension (single arrows); (b) cultural adaptation of language to the brain (double arrows), resulting in increasingly expressive languages (curved arrows) that are well suited to being acquired and processed by domain-general mechanisms (single arrows).

Instead of puzzling that humans can only learn a small subset of the infinity of mathematically possible languages, we take a different starting point: the observation that natural languages exist only because humans can produce, learn, and process them. In order for languages to be passed on from generation to generation, they must adapt to the properties of the human learning and processing mechanisms; the structures in each language form a highly interdependent *system*, rather than a collection of independent traits. The key to understanding the fit between language and the brain is to understand how language has been shaped by the brain, not the reverse. The process by which language has been shaped by the brain is, in important ways, akin to Darwinian selection. Hence, we suggest that it is a productive metaphor to view languages as analogous to biological species, adapted through natural selection to fit a particular ecological niche: the human brain.

This viewpoint does not rule out the possibility that language may have played a role in the biological evolution of hominids. Good language skills may indeed enhance reproductive success. But the pressures working on language to adapt to humans are significantly stronger than the selection pressures on humans to use language. In case of the former, a language can *only* survive if it is learnable and processable by humans. On the other hand, adaptation towards language use is merely *one of many* selective pressures working on hominid evolution (including, for example, avoiding predators and finding food). Whereas humans can survive without language, the opposite is not the case. Thus, prima facie language is more likely to have been shaped to fit the human brain rather than the other way round. Languages that are hard for humans to learn and process cannot come into existence at all.

5.1. Historical parallels between linguistic and biological change

The idea of language as an adaptive, evolutionary system has a prominent historical pedigree dating back to Darwin and beyond. One of the earliest proponents of the idea that languages evolve diachronically was the eighteenth-century language scholar, Sir William Jones, the first Western scholar to study Sanskrit and note its affinity with Greek and Latin (Cannon 1991). Later, nineteenth-century linguistics was dominated by an organistic view of language (McMahon 1994). Franz Bopp, one of the founders of comparative linguistics, regarded language as an organism that could be dissected and classified (Davies 1987). Wilhelm von Humboldt, the father of generative grammar (Chomsky 1965; Pinker 1994), argued that "language, in direct conjunction with mental power, is a fully-fashioned *organism*" (von Humboldt 1836/1999, p. 90; original emphasis). More generally, languages were viewed as having lifecycles that included birth, progressive growth, procreation, and eventually decay and death. However, the notion of evolution underlying this organistic view of language was largely pre-Darwinian. This is perhaps reflected most clearly in the writings of another influential linguist, August Schleicher. Although he explicitly emphasized the relationship between linguistics and Darwinian theory (Schleicher 1863, quoted in Percival 1987), Darwin's principles of mutation, variation, and natural selection did not enter into the theorizing about language evolution (Nerlich 1989). Instead, the evolution of language was seen in pre-Darwinian terms as the progressive growth towards attainment of perfection, followed by decay.

Darwin (1874), too, recognized the similarities between linguistic and biological change[12]:

> The formation of different languages and of distinct species, and the proofs that both have been developed through a gradual process, are curiously parallel . . . We find in distinct languages striking homologies due to community of descent, and analogies due to a similar process of formation. The manner in which certain letters or sounds change when others change is very like correlated growth . . . Languages, like organic beings, can be classed in groups under groups; and they can be classed either naturally, according to descent, or artificially by other characters. Dominant languages and dialects spread widely, and lead to the gradual extinction of other tongues. A language, like a species, when once extinct, never . . . reappears . . . A struggle for life is constantly going on among the words and grammatical forms in each language. The better, the shorter, the easier forms are constantly gaining the upper hand . . . The survival and preservation of certain favored words in the struggle for existence is natural selection. (p. 106)

In this sense, natural language can be construed metaphorically as akin to an organism whose evolution has been constrained by the properties of human learning and processing mechanisms. A similar perspective on language evolution was revived, within a modern evolutionary framework, by Stevick (1963) and later by Nerlich (1989). Sereno (1991) has listed a number of parallels between biological organisms and language (with the biological comparisons in parentheses):

> An intercommunicating group of people defines a language (cf. gene flow in relation to a species); language abilities develop in each speaker (cf. embryonic development); language must be transmitted to offspring (cf. heritability); there is a low level process of sound and meaning change that continuously generates variation (cf. mutation); languages gradually diverge, especially when spatially separated (cf. allopatric speciation); geographical distributions of dialects (cf. subspecies, clines) gradually give rise to wholesale rearrangements of phonology and syntax (cf. macroevolution); sociolinguistic isolation can lead to language divergence without spatial discontinuity (cf. sympatric speciation). (Sereno 1991, p. 472)

Christiansen (1994) pushed the analogy a little further, suggesting that language may be viewed as a "beneficial parasite" engaged in a symbiotic relationship with its human hosts, without whom it cannot survive (see also Deacon 1997). Symbiotic parasites and their hosts tend to become increasingly co-adapted (e.g., Dawkins 1976). But note that this co-adaptation will be very lopsided, because the rate of linguistic change is far greater than the rate of biological change. Whereas Danish and Hindi needed less than 7,000 years to evolve from a common hypothesized proto-Indo-European ancestor into very different languages (Gray & Atkinson 2003), it took our remote ancestors approximately 100,000–200,000 years to evolve from the archaic form of *Homo sapiens* into the anatomically modern form, sometimes termed *Homo sapiens sapiens*. Indeed, as we argued in section 3, the rapidity of language change – and the geographical dispersal of humanity – suggests that biological adaptation to language is negligible. This suggestion is further corroborated by work in evolutionary game theory, showing that

when two species with markedly different rates of adaptation enter a symbiotic relationship, the rapidly evolving species adapts to the slowly evolving one, but not the reverse (Frean & Abraham 2004).

5.2. Language as a system

But in what sense should language be viewed as akin to an integrated *organism*, rather than as a collection of separate traits, evolving relatively independently? The reason is that language is highly *systematic* – so much so, indeed, that much of linguistic theory is concerned with tracking the systematic relationships among different aspects of linguistic structure. Although language is an integrated system, it can, nonetheless, be viewed as comprising a complex set of "features" or "traits" which may or may not be passed on from one generation to the next (concerning lexical items, idioms, aspects of phonology, syntax, and so on). To a first approximation, traits that are easy for learners to acquire and use will become more prevalent; traits that are more difficult to acquire and use will disappear. Thus, selectional pressure from language learners and users will shape the way in which language evolves. Crucially, the systematic character of linguistic traits means that, to some degree at least, the fates of different traits in a language are intertwined. That is, the degree to which any particular trait is easy to learn or process will, to some extent, depend on the other features of the language – because language users will tend to learn and process each aspect of the language in light of their experience with the rest. This picture is familiar in biology – the selectional impact of any gene depends crucially on the rest of the genome; the selectional forces on each gene, for good or ill, are tied to the development and functioning of the entire organism.

Construing language as an evolutionary system has implications for explanations of *what* is being selected in language evolution. From the viewpoint of generative grammar, the unit of selection would seem to be either specific UG principles (in PPT; Newmeyer 1991), particular parts of the UG toolkit (in SS; Culicover & Jackendoff 2005), or recursion in the form of Merge (in MP; Hauser et al. 2002). In all cases, selection would seem to take place at a high level of abstraction that cuts across a multitude of specific linguistic constructions. Our approach suggests a different perspective inspired by the "lexical turn" in linguistics (e.g., Combinatory Categorical Grammar, Steedman 2000; Head-driven Phrase Structure Grammar, Sag & Pollard 1987; Lexical-Functionalist Grammar, Bresnan 1982), focusing on specific lexical items with their associated syntactic and semantic information. Specifically, we adopt a Construction Grammar view of language (e.g., Croft 2000; 2001; Goldberg 2006; O'Grady 2005), proposing that individual constructions consisting of words or combinations thereof are among the basic units of selection.

To spell out the parallel, the idiolect of an individual speaker is analogous to an individual organism; a language (e.g., Mandarin, French) is akin to a species. A linguistic "genotype" corresponds to the neural representation of an idiolect, instantiated by a collection of mental "constructions," which are here analogous to genes, and gives rise to linguistic behavior – the language "phenotype" – characterized by a collection of utterances and interpretations. Just as the fitness of an individual gene depends on its interaction with other genes, so the fitness of an individual construction is intertwined with those of other constructions; that is, constructions are part of a (linguistic) system. A species in biology is defined by the ability to interbreed; a "language species" is defined by mutual intelligibility. Hence, interbreeding and mutually intelligible linguistic interactions can be viewed as analogous processes by which genetic material and constructions can propagate.

The long-term survival of any given construction is affected both by its individual properties (e.g., frequency of usage) and how well it fits into the overall linguistic system (e.g., syntactic, semantic, or pragmatic overlap with other constructions). In a series of linguistic and corpus-based analyses, Bybee (2007) has shown how frequency of occurrence plays an important role in shaping language from phonology to morphology to morphosyntax, due to the effects of repeated processing experiences with specific examples (either types or tokens). Additionally, groups of constructions overlapping in terms of syntactic, semantic, and/or pragmatic properties emerge and form the basis for usage-based generalizations (e.g., Goldberg 2006; Tomasello 2003). Crucially, however, these groupings lead to a distributed system of *local* generalizations across partially overlapping constructions, rather than the abstract, mostly global generalizations of current generative grammar.

In psycholinguistics, the effects of frequency and pattern overlap have been observed in so-called Frequency × Regularity interactions. As an example, consider the acquisition of the English past tense. Frequently occurring mappings, such as *go* → *went*, are learned more easily than more infrequent mappings, such as *lie* → *lay*. However, low-frequency patterns may be more easily learned if they overlap in part with other patterns. Thus, the partial overlap in the mappings from stem to past tense in *sleep* → *slept, weep* → *wept, keep* → *kept* (i.e., *-eep* → *-ept*) make the learning of the these mappings relatively easy even though none of the words individually have a particularly high frequency. Importantly, the two factors – frequency and regularity (i.e., degree of partial overlap) – interact with each other. High-frequency patterns are easily learned independent of whether they are regular or not, whereas the learning of low-frequency patterns suffers if they are not regular (i.e., if they do not have partial overlap with other patterns). Results from psycholinguistic experimentation and computational modeling have observed such Frequency × Regularity interactions across many aspects of language, including auditory word recognition (Lively et al. 1994), visual word recognition (Seidenberg 1985), English past tense acquisition (Hare & Elman 1995), and sentence processing (Juliano & Tanenhaus 1994; MacDonald & Christiansen 2002; Pearlmutter & MacDonald 1995).

In our case, we suggest that similar interactions between frequency and pattern overlap are likely to play an important role in language evolution. Individual constructions may survive through frequent usage or because they participate in usage-based generalizations through syntactic, semantic, or pragmatic overlap with other similar constructions. Additional support for this suggestion comes from artificial language learning studies with human subjects, demonstrating that certain combinations of artificial-language structures are more easily learned than others given sequential learning biases (e.g., Christiansen 2000; Reeder 2004;

Saffran 2001; and see sect. 6.3 of this target article). For example, Ellefson and Christiansen (2000) compared human learning across two artificial languages that only differed in the order of words in two out of six sentence types. They found that not only was the more "natural" language learned better overall, but also that the four sentence types common to both languages were learned better as well. This suggests that the artificial languages were learned as integrated systems, rather than as collections of independent items.

Further corroboration comes from a study by Kaschak and Glenberg (2004) who had adult participants learn the *needs* construction (e.g., "The meal needs cooked"), a feature of the American English dialect spoken in the northern midlands region from western Pennsylvania across Ohio, Indiana, and Illinois to Iowa. The training on the needs construction facilitated the processing of related modifier constructions (e.g., "The meal needs cooked vegetables"), again suggesting that constructions form an integrated system that can be affected by the learning of new constructions. Thus, although constructions are selected independently, they also provide an environment for each other within which selection takes place, just as the selection of individual genes are tied to the survival of the other genes that make up an organism.

5.3. The nature of language universals

We have argued that language is best viewed as a linguistic system adapted to the human brain. But if evolution is unlikely to have bestowed us with an innate UG, then how can we account for the various aspects of language that UG constraints are supposed to explain? That is, how can we explain the existence of apparent language universals, in the form of regularities in language structure and use? Notice, however, that is it by no means clear exactly what counts as a language universal. Rather, the notion of language universals differs considerably across language researchers (e.g., the variety in perspectives among contributions in Christiansen et al., in press). Many linguists working within the generative grammar framework see universals as primarily, and sometimes exclusively, deriving from UG (e.g., Hornstein & Boeckx, in press; Pinker & Jackendoff, in press). Functional linguists, on the other hand, view universals as arising from patterns of language usage due to pragmatic, processing, and other constraints, and amplified in diachronic language change (e.g., Bybee, in press). However, even within the same theoretical linguistic framework, there is often little agreement about what the exact universals are. For example, when surveying specific universals proposed by different proponents of UG, Tomasello (2004) found little overlap among proposed universals.

Although there may be little agreement about specific universals, some consensus can nonetheless be found with respect to their general nature. Thus, within mainstream generative grammar approaches, including MP and PPT, language universals are seen as arising from the inner workings of UG. Hornstein and Boeckx (in press) refer to such UG-based universals as internalist or I-Universals. They note that:

> on this conception I-Universals are likely to be (and have been found to be) quite abstract. They need not be observable. Thus, even were one to survey thousands of languages looking for commonalities, they could easily escape detection. In this they contrast with Greenbergian Universals, which we would call E(xternalist)-Universals. In fact, on this conception, the mere fact that every language displayed some property P does not imply that P is a universal in the I-sense. Put more paradoxically, the fact that P holds universally does not imply that P is a universal. Conversely, some property can be an I-Universal even if only manifested in a single natural language. The only thing that makes something an I-Universal on this view is that it is a property of our innate ability to grow a language (p. 4).

Thus, from the perspective of MP and PPT, language universals are by definition properties of UG; that is, they are *formal* universals (Chomsky 1965). A similar view of universals also figures within the SS framework (Culicover & Jackendoff 2005), defined in terms of the universal toolkit encoded in UG. Because different languages are hypothesized to use different subsets of tools, the SS approach – like MP and PPT – suggests that some universals may not show up in all languages (Pinker & Jackendoff, in press). However, both notions of universals face the logical problem of language evolution discussed above (in sects. 2–4): How could the full set of UG constraints have evolved if any single linguistic environment only ever supported a subset of them?

The solution to this problem, we suggest, is to adopt a non-formal conception of universals in which they emerge from processes of repeated language acquisition and use. We see universals as products of the interaction among constraints deriving from the way our thought processes work, from perceptuo-motor factors, from cognitive limitations on learning and processing, and from pragmatic sources (see sect. 6 below). This view implies that most universals are unlikely to be found across all languages; rather, "universals" are more akin to statistical trends tied to patterns of language use. Consequently, specific universals fall on a continuum ranging from being attested to only in some languages to being found across most languages. An example of the former is the class of implicational universals, such as that verb-final languages tend to have postpositions (Dryer 1992), whereas the presence of nouns and verbs in most, if not all, languages (minimally as typological prototypes; Croft 2001) is an example of the latter. Thus, language universals, we suggest, are best construed as statistical tendencies with varying degrees of universality across the world's languages.

We have argued that language is too variable, both in time and space, to provide a selectional pressure that might shape the gradual adaptation of an innate UG encoding arbitrary, but universal linguistic constraints. Moreover, a putative innate UG would be too complex and specialized to have credibly arisen through non-adaptationist mechanisms. Instead, we have proposed that the fit between language and the brain arises because language has evolved to be readily learned and processed by the brain. We now consider what kinds of non-linguistic constraints are likely to have shaped language to the brain, and given rise to statistical tendencies in language structure and use.

6. Constraints on language structure

We have proposed that language has adapted to the non-linguistic constraints deriving from language learners and users, giving rise to observable linguistic universals. But how far can these constraints be identified? To what extent can linguistic structure previously ascribed to an innate UG be identified as having a non-linguistic basis? Clearly, establishing a complete answer to this question would require a vast program of research. In this section, we illustrate how research from different areas of the language sciences can be brought together to explain aspects of language previously thought to require the existence of UG for their explanation. For the purpose of exposition, we divide the constraints into four groups relating to thought, perceptuo-motor factors, cognition, and pragmatics. These constraints derive from the limitations and idiosyncratic properties of the human brain and other parts of our body involved in language (e.g., the vocal tract). However, as we note further on in section 6.5, any given linguistic phenomenon is likely to arise from a combination of multiple constraints that cut across these groupings, and, thus, across different kinds of brain mechanisms.

6.1. Constraints from thought

The relationship between language and thought is potentially abundantly rich, but also extremely controversial. Thus, the analytic tradition in philosophy can be viewed as attempting to understand thought through a careful analysis of language (e.g., Blackburn 1984). It has been widely assumed that the structure of sentences (or utterances, and perhaps the contexts in which they stand), and the inferential relations over them, provide an analysis of thought. A standard assumption is that thought is largely prior to, and independent of, linguistic communication. Accordingly, fundamental properties of language, such as compositionality, function-argument structure, quantification, aspect, and modality, may arise from the structure of the thoughts language is required to express (e.g., Schoenemann 1999).

Presumably, language also provides a reasonably efficient mapping of the mental representation of thoughts, with these properties, into phonology. This viewpoint can be instantiated in a variety of ways. For example, Steedman's emphasis on incremental interpretation (e.g., that successive partial semantic representations are constructed as the sentence unfolds – i.e., the thought that a sentence expresses is built up piecemeal) is one motivation for categorical grammar (e.g., Steedman 2000). From a very different stance, the aim of finding a "perfect" relationship between thought and phonology is closely related to the goals of the Minimalist Program (Chomsky 1995).[13] Indeed, Chomsky has recently suggested (e.g., Chomsky 2005b) that language may have originated as a vehicle for thought and only later became exapted to serve as a system of communication. This viewpoint would not, of course, explain the content of a putative UG, which concerns principles for mapping mental representations of thought into phonology; and this mapping surely *is* specific to communication: inferences are, after all, presumably defined over mental representations of thoughts, rather than phonological representations, or, for that matter, syntactic trees.

The lexicon is presumably also strongly constrained by processes of perception and categorization – the meanings of words must be both learnable and cognitively useful (e.g., Murphy 2002). Indeed, the philosophical literature on lexical meaning, from a range of theoretical perspectives, sees cognitive constraints as fundamental to understanding word meaning, whether these constraints are given by innate systems of internal representation (Fodor 1975) or primitive mechanisms of generalization (Quine 1960). Cognitive linguists (e.g., Croft & Cruise 2004) have argued for a far more intimate relation between thought and language:. For example, basic conceptual machinery (e.g., concerning spatial structure) and the mapping of such structure into more abstract domains (e.g., via metaphor) are, according to some accounts, evident in languages (e.g., Lakoff & Johnson 1980). And from a related perspective (e.g., Croft 2001), some linguists have argued that semantic categories of thought (e.g., of objects and relations) may be shared between languages, whereas syntactic categories and constructions are defined by language-internal properties, such as distributional relations, so that the attempt to find cross-linguistic syntactic universals is doomed to failure.

6.2. Perceptuo-motor constraints

The motor and perceptual machinery underpinning language seems inevitably to have some influence on language structure. The seriality of vocal output, most obviously, forces a sequential construction of messages. A perceptual and memory system that is typically a "greedy" processor, and has a very limited capacity for storing "raw" sensory input of any kind (e.g., Haber 1983), may, moreover, force a code which can be interpreted incrementally (rather than the many practical codes in communication engineering, in which information is stored in large blocks, e.g., Mackay 2003). The noisiness and variability (both with context and speaker) of vocal – or, indeed, signed – signals may, moreover, force a "digital" communication system, with a small number of basic messages: that is, one that uses discrete units (phonetic features or phonemes).

The basic phonetic inventory is transparently related to deployment of the vocal apparatus, and it is also possible that it is tuned, to some degree, to respect "natural" perceptual boundaries (Kuhl 1987). Some theorists have argued for more far-reaching connections. For example, MacNeilage (1998) argues that aspects of syllable structure emerge as a variation on the jaw movements involved in eating; and for some cognitive linguists, the perceptual-motor system is a crucial part of the machinery on which the linguistic system is built (e.g., Hampe 2006). The depth of the influence of perceptual and motor control on more abstract aspects of language is controversial, but it seems plausible that such influence may be substantial.

6.3. Cognitive constraints on learning and processing

In our framework, language acquisition is construed not as learning a distant grammar, but as learning how to *process* language. Although constraints on learning and processing are often treated separately (e.g., Bybee 2007; Hawkins 2004; Tomasello 2003), we see them as being highly

intertwined, subserved by the very same underlying mechanisms. Language processing involves extracting regularities from highly complex sequential input, pointing to a connection between general sequential learning (e.g., planning, motor control, etc.; Lashley 1951) and language: both involve the extraction and further processing of discrete elements occurring in complex temporal sequences. It is therefore not surprising that sequential learning tasks have become an important experimental paradigm for studying language acquisition and processing (sometimes under the heading of "artificial grammar/ language learning" [Gómez & Gerken 2000] or "statistical learning" [Saffran 2003]). Sequential learning has thus been demonstrated for a variety of different aspects of language, including: speech segmentation (Curtin et al. 2005; Saffran et al. 1996a; 1996b); discovering complex word-internal structure between nonadjacent elements (Newport & Aslin 2004; Onnis et al. 2005; Peña et al. 2002); acquiring gender-like morphological systems (Brooks et al. 1993; Frigo & McDonald 1998); locating syntactic phrase boundaries (Saffran 2001; 2002); using function words to delineate phrases (Green 1979); integrating prosodic and morphological cues in the learning of phrase structure (Morgan et al. 1987); integrating phonological and distributional cues (Monaghan et al. 2005); and detecting long-distance relationships between words (Gómez 2002; Onnis et al. 2003).

The close relationship between sequential learning and grammatical ability has been further corroborated by recent neuroimaging studies, showing that people trained on an artificial language have the same event-related potential (ERP) brainwave patterns to ungrammatical artificial-language sentences as to ungrammatical natural-language sentences (Christiansen et al. 2007; Friederici et al. 2002). Moreover, novel incongruent musical sequences elicit ERP patterns that are statistically indistinguishable from syntactic incongruities in language (Patel et al. 1998). Results from a magnetoencephalography (MEG) experiment further suggest that Broca's area plays a crucial role in processing music sequences (Maess et al. 2001). Finally, event-related functional magnetic resonance imaging (fMRI) has shown that the same brain area – Broca's area – is involved in an artificial grammar learning task and in normal natural language processing (Petersson et al. 2004). Further evidence comes from behavioral studies with language-impaired populations, showing that aphasia (Christiansen et al., submitted; Hoen et al. 2003), language learning disability (Plante et al. 2002), and specific language impairment (Hsu et al. 2006; Tomblin et al. 2007) are associated with impaired sequential learning. Together, these studies strongly suggest that there is considerable overlap in the neural mechanisms involved in language and sequential learning[14] (see also Conway et al. 2007; Ullman 2004; Wilkins & Wakefield 1995, for similar perspectives).

This psychological research can be seen as a foundation for work in functional and typological linguistics, indicating how theoretical constraints on sequential learning and processing can explain certain universal patterns in language structure and use. One suggestion, from O'Grady (2005), is that the language processing system seeks to resolve linguistic dependencies (e.g., between verbs and their arguments) at the first opportunity – a tendency that might not be syntax-specific, but, instead, an instance of a general cognitive tendency to attempt to resolve ambiguities rapidly in linguistic (Clark 1975) and perceptual input (Pomerantz & Kubovy 1986). In a similar vein, Hawkins (1994; 2004) and Culicover (1999) propose specific measures of processing complexity (roughly, the number of linguistic constituents required to link syntactic and conceptual structure), which they assume underpin judgments concerning linguistic acceptability. The collection of studies in Bybee (2007) further underscores the importance of frequency of use in shaping language. Importantly, these lines of work have begun to detail learning and processing constraints that can help explain specific linguistic patterns, such as the aforementioned examples of pronoun binding (previous Examples 1–4; see O'Grady 2005) and heavy NP-shift (Examples 5–6; see Hawkins 1994; 2004), and indicate an increasing emphasis on performance constraints within linguistics.

In turn, a growing body of empirical research in computational linguistics, cognitive science, and psycholinguistics has begun to explore how these theoretical constraints may be instantiated in terms of computational and psychological mechanisms. For instance, basic word order patterns may thus derive from memory constraints related to sequential learning and processing of linguistic material, as indicated by computational simulations (e.g., Christiansen & Devlin 1997; Kirby 1999; Lupyan & Christiansen 2002; Van Everbroeck 1999), human experimentation involving artificial languages (e.g., Christiansen 2000; Reeder 2004), and cross-linguistic corpus analyses (e.g., Bybee 2002; Hawkins 1994; 2004). Similarly, behavioral experiments and computational modeling have provided evidence for general processing constraints (instead of innate subjacency constraints) on complex question formation (Berwick & Weinberg 1984; Ellefson & Christiansen 2000).

6.4. Pragmatic constraints

Language is likely, moreover, to be substantially shaped by the pragmatic constraints involved in linguistic communication. The program of developing and extending Gricean implicatures (Grice 1967; Levinson 2000; Sperber & Wilson 1986) has revealed enormous complexity in the relationship between the literal meaning of an utterance and the message that the speaker intends to convey. Pragmatic processes may, indeed, be crucial in understanding many aspects of linguistic structure, as well as the processes of language change.

Consider the nature of anaphora and binding. Levinson (2000) notes that the patterns of "discourse" anaphora, Example (7), and syntactic anaphora, Example (8), have interesting parallels.

7. a. John arrived. He began to sing.
   b. John arrived. The man began to sing.
8. a. John arrived and he began to sing.
   b. John arrived and the man began to sing.

In both (7) and (8), the first form indicates preferred co-reference of *he* and *John*; the second form prefers non-coreference. The general pattern is that brief expressions encourage co-reference with a previously introduced item; Grice's maxim of quantity implies that, by default, a prolix expression will not be used where a

brief expression could be, and hence prolix expressions are typically taken to imply non-coreference with previously introduced entities. Where the referring expression is absent, then co-reference may be required as in Example (9), in which the singer can only be John:

9. John arrived and began to sing.

It is natural to assume that syntactic structures emerge, diachronically, from reduction of discourse structures – and that, in Givón's phrase, "Yesterday's discourse is today's syntax" (as cited in Tomasello 2008). The shift, over time, from default constraint to rigid rule is widespread in language change and much studied in the subfield of grammaticalization (see sect. 7.1).

Applying this pragmatic perspective to the binding constraints, Levinson (1987a; 1987b; 2000) notes that the availability, but non-use, of the reflexive *himself* provides a default (and later, perhaps, rigid) constraint that *him* does not co-refer with *John* in Example (10).

10. a. John_i likes himself_i.
    b. John_i likes him_j.

Levinson (2000), building on related work by Reinhart (1983), provides a comprehensive account of the binding constraints, and putative exceptions to them, purely on pragmatic principles (see also Huang 2000, for a cross-linguistic perspective). In sum, pragmatic principles can at least partly explain both the structure and origin of linguistic patterns that are often viewed as solely formal and, hence, arbitrary.

6.5. The impact of multiple constraints

In section 6 so far, we have discussed four types of constraints that have shaped the evolution of language. Importantly, we see these constraints as interacting with one another, such that individual linguistic phenomena arise from a combination of several different types of constraints. For example, the patterns of binding phenomena are likely to require explanations that cut across the four types of constraints, including constraints on cognitive processing (O'Grady 2005) and pragmatics (Levinson 1987a; Reinhart 1983). That is, the explanation of any given aspect of language is likely to require the inclusion of multiple overlapping constraints deriving from thought, perceptual-motor factors, cognition, and pragmatics.

The idea of explaining language structure and use through the integration of multiple constraints goes back at least to early functionalist approaches to the psychology of language (e.g., Bates & MacWhinney 1979; Bever 1970; Slobin 1973). It plays an important role in current constraint-based theories of sentence comprehension (e.g., MacDonald et al. 1994; Tanenhaus & Trueswell 1995). Experiments have demonstrated how adults' interpretations of sentences are sensitive to a variety of constraints, including specific world knowledge relating to the content of an utterance (e.g., Kamide et al. 2003), the visual context in which the utterance is produced (e.g., Tanenhaus et al. 1995), the sound properties of individual words (Farmer et al. 2006), the processing difficulty of an utterance as well as how such difficulty may be affected by prior experience (e.g., Reali & Christiansen 2007), and various pragmatic factors (e.g., Fitneva & Spivey 2004). Similarly, the integration of multiple constraints, or "cues," also figures prominently in contemporary theories of language acquisition (see e.g., contributions in Golinkoff et al. 2000; Morgan & Demuth 1996; Weissenborn & Höhle 2001; for a review, see Monaghan & Christiansen 2008).

The multiple-constraints satisfaction perspective on language evolution also offers an explanation of why language is unique to humans: As a cultural product, language has been shaped by constraints from multiple mechanisms, some of which have properties unique to humans. Specifically, we suggest that language does not involve any qualitatively different mechanisms compared to extant apes, but instead a number of quantitative evolutionary refinements of older primate systems (e.g., for intention sharing and understanding, Tomasello et al. 2005; or complex sequential learning and processing,[15] Conway & Christiansen 2001). These changes could be viewed as providing necessary pre-adaptations that, once in place, allowed language to emerge through cultural transmission (e.g., Elman 1999). It is also conceivable that initial changes, if functional, could have been subject to further amplification through the Baldwin effect, perhaps resulting in multiple quantitative shifts in human evolution. The key point is that none of these changes would result in the evolution of UG. The species-specificity of a given trait does not necessitate postulating specific biological adaptations for that trait. For example, even though playing tag may be species-specific and perhaps even universal, few people, if any, would argue that humans have evolved specific adaptations for playing this game. Thus, the uniqueness of language is better viewed as part of the larger question: Why are humans different from other primates? It seems clear that considering language in isolation is not going to give us the answer to this question.

7. How constraints shape language over time

According to the view that language evolution is determined by the development of UG, there is a sharp divide between questions of language evolution (how the genetic endowment could arise evolutionarily) and historical language change (which is viewed as variation within the genetically determined limits of possible human languages). By contrast, if language has evolved to fit prior cognitive and communicative constraints, then it is plausible that historical processes of language change provide a model of language evolution; indeed, historical language change may be language evolution in microcosm. This perspective is consistent with much work in functional and typological linguistics (e.g., Bever & Langendoen 1971; Croft 2000; Givón 1998; Hawkins 2004; Heine & Kuteva 2002).

At the outset, it is natural to expect that language will be the outcome of competing selectional forces. On the one hand, as we shall note, there will be a variety of selectional forces that make the language "easier" for speakers/hearers; on the other, it is likely that expressibility is a powerful selectional constraint, tending to increase linguistic complexity over evolutionary time. For instance, it has been suggested that the use of hierarchical structure and limited recursion to express more complex meanings may have arrived at later stages of language evolution (Jackendoff 2002; Johansson 2006). Indeed, the modern Amazonian language, Pirahã, lacks recursion and has one of the world's smallest phoneme inventories (though its morphology is complex), limiting its expressivity (Everett

2005; but see also the critique by Nevins et al. 2007, and Everett's 2007 response).

While expressivity is one selectional force that may tend to increase linguistic complexity, it will typically stand in opposition to another: ease of learning and processing will tend to favor linguistic simplicity. But the picture may be more complex: in some cases, ease of learning and ease of processing may stand in opposition. For example, regularity makes items easier to *learn*; the shortening of frequent items, and consequent irregularity, may make aspects of language easier to *say*. There are similar tensions between ease of production (which favors simplifying the speech signal) and ease of comprehension (which favors a richer, and hence more informative, signal). Moreover, whereas constraints deriving from the brain provide pressures toward simplification of language, processes of grammaticalization can add complexity to language (e.g., by the emergence of morphological markers). Thus, part of the complexity of language, just as in biology, may arise from the complex interaction of competing constraints.

7.1. Language evolution as linguistic change

Recent theory in diachronic linguistics has focused on grammaticalization (e.g., Bybee et al. 1994; Heine 1991; Hopper & Traugott 1993): the process by which functional items, including closed class words and morphology, develop from what are initially open-class items. This transitional process involves a "bleaching" of meaning, phonological reduction, and increasingly rigid dependencies with other items. Thus, the English number *one* is likely to be the root to *a*(*n*). The Latin *cantare habeo* (*I have* [something] *to sing*) mutated into *chanterais*, *cantaré, cantarò* (*I will sing* in French, Spanish, Italian). The suffix corresponds phonologically to *I have* in each language (respectively, *ai*, *he*, *ho* – the *have* element has collapsed into inflectional morphology; Fleischman 1982). The same processes of grammaticalization can also cause certain content words over time to get bleached of their meaning and become grammatical particles. For example, the use of *go* and *have* as auxiliary verbs (as in *I am going to sing* or *I have forgotten my hat*) have been bleached of their original meanings concerning physical movement and possession (Bybee et al. 1994). The processes of grammaticalization appear gradual and follow historical patterns, suggesting that there are systematic selectional pressures operative in language change. More generally, these processes provide a possible origin of grammatical structure from a proto-language initially involving perhaps unordered and uninflected strings of content words.

From a historical perspective, it is natural to view many aspects of syntax as emerging from processing or pragmatic factors. Revisiting our discussion of binding constraints, we might view complementary distributions of reflexive and non-reflexive pronouns as initially arising from pragmatic factors; the resulting pattern may be acquired and modified by future generations of learners, to some degree independently of those initial factors (e.g., Givón 1979; Levinson 1987b). Thus, binding constraints might be a complex product of many forces, including pragmatic factors, and learning and processing biases – and hence, the subtlety of those constraints should not be entirely surprising. But from the present perspective, the fact that such a complex system of constraints is readily learnable, is neither puzzling, nor indicative of an innately specified genetic endowment. Rather, the constraints are learnable because they have been shaped by the very pragmatic, processing and learning constraints with which the learner is endowed.

Understanding the cognitive and communicative basis for the direction of grammaticalization and related processes is an important challenge. But equally, the suggestion that this type of observable historical change may be continuous with language evolution opens up the possibility that research on the origin of language may not be a theoretically isolated island of speculation, but may connect directly with one of the most central topics in linguistics: the nature of language change (e.g., Zeevat 2006). Indeed, grammaticalization has become the center of many recent perspectives on the evolution of language as mediated by cultural transmission across hundreds, perhaps thousands, of generations of learners (e.g., Bybee et al. 1994; Givón 1998; Heine & Kuteva 2002; Schoenemann 1999; Tomasello 2003). Although the present approach also emphasizes the importance of grammaticalization in the evolution of complex syntax, it differs from other approaches in that we see this diachronic process as being constrained by limitations on learning and processing. Indeed, there have even been intriguing attempts to explain some aspects of language change with reference to the learning properties of connectionist networks. For example, Hare and Elman (1995) demonstrated how cross-generational learning by sequential learning devices can model the gradual historical change in English verb inflection from a complex past tense system in Old English to the dominant "regular" class and small classes of "irregular" verbs of modern English.

7.2. Language evolution through cultural transmission

How far can language evolution and historical processes of language change be explained by general mechanisms of cultural transmission? And how might language be selectively distorted by such processes? Crucial to any such model are assumptions about the channel over which cultural information is transmitted, the structure of the network of social interactions over which transmission occurs, and the learning and processing mechanisms that support the acquisition and use of the transmitted information (Boyd & Richerson 2005).

A wide range of recent computational models of the cultural transmission of language has been developed, with different points of emphasis. Some of these models have considered how language is shaped by the process of transmission over successive generations, by the nature of the communication problem to be solved, and/or by the nature of the learners (e.g., Batali 1998; Kirby 1999). For example, Kirby et al. (2007) show that, if information is transmitted directly between individual learners, and learners sample grammars from the Bayes posterior distribution of grammars, given that information, then language asymptotically converges to match the priors initially encoded by the learners. In contrast, Smith et al. (2003a), using a different model of how information is learned, indicate how compositional structure in language might have resulted from the complex interaction of learning constraints and cultural

transmission, resulting in a "learning bottleneck." Moreover, a growing number of studies have started to investigate the potentially important interactions between biological and linguistic adaptation in language evolution (e.g., Christiansen et al. 2006; Hurford 1990; Hurford & Kirby 1999; Kvasnicka & Pospichal 1999; Livingstone & Fyfe 2000; Munroe & Cangelosi 2002; Smith 2002; 2004; Yamauchi 2001).

Of particular interest here are simulations indicating that apparently arbitrary aspects of linguistic structure may arise from constraints on learning and processing (e.g., Kirby 1998; 1999; Van Everbroeck 1999). For example, it has been suggested that subjacency constraints may arise from cognitive limitations on sequential learning (Ellefson & Christiansen 2000). Moreover, using rule-based language induction, Kirby (1999) accounted for the emergence of typological universals as a result of domain-general learning and processing constraints. Finally, note that, in line with the present arguments, a range of recent studies have challenged the plausibility of biological adaptation to arbitrary features of the linguistic environment (e.g., Christiansen et al. 2006; Kirby & Hurford 1997; Kirby et al. 2007; Munroe & Cangelosi 2002; Yamauchi 2001).

The range of factors known to be important in cultural transmission (e.g., group size and networks of transmission among group members, fidelity of transmission) has been explored relatively little in simulation work. Furthermore, to the extent that language is shaped by the brain, enriching the models of cultural transmission of language against the backdrop of learning and processing constraints, will be an important direction for the study both of historical language change and language evolution. More generally, viewing language as shaped by cultural transmission (Arbib 2005; Bybee 2002; Donald 1998) only provides the starting point for an explanation of linguistic regularities. The real challenge, we suggest, is to delineate the wide range of constraints, from perceptuo-motor to pragmatic (as sketched earlier in sect. 6), that operate on language evolution. Detailing these constraints is likely to be crucial for explanations of complex linguistic regularities, and how they can readily be learned and processed.

We note here that this perspective on the adaptation of language differs importantly from the processes of cultural change that operate through deliberate and conscious innovation and/or evaluation of cultural variants. On our account, the processes of language change operate to make languages easier to learn and process, and more communicatively effective. But these changes do not operate through processes either of "design" or deliberate adoption by language users. Thus, following Darwin, we view the origin of the adaptive complexity in language as analogous to the origin of adaptive complexity in biology. Specifically, the adaptive complexity of biological organisms is presumed to arise from random genetic variation, winnowed by natural selection (a "blind watchmaker"; Dawkins 1986). We argue that the adaptive complexity of language arises, similarly, from random linguistic variation winnowed by selectional pressures, though here concerning learning and processing (so again, we have a *blind* watchmaker).

By contrast, for aspects of cultural changes for which variants are either created, or selected, by deliberate choice, the picture is very different. Such cultural products can be viewed instead as arising from the incremental action of processes of intelligent design, and more or less explicit evaluations, and decisions to adopt (see Chater 2005). Many phenomena discussed by evolutionary theorists concerning culture (e.g., Campbell 1965; Richerson & Boyd 2005) – including those described by meme-theorists (e.g., Blackmore 1999; Dawkins 1976; Dennett 1995) – fall into this latter category. Explanations of fashions (e.g., wearing baseball caps backwards), catch-phrases, memorable tunes, engineering methods, cultural conventions and institutions (e.g., marriage, revenge killings), scientific and artistic ideas, religious views, and so on, seem patently to be products of *sighted* watchmakers; that is, they are products, in part at least, of many generations of intelligent designers, imitators, and critics.

Our focus here concerns, instead, the specific and interdependent constraints which operate on particular linguistic structures and of which people have no conscious awareness. Presumably, speakers do not deliberately contemplate syntactic reanalyses of existing structures, bleach the meaning of common verbs so that they play an increasingly syntactic role, or collapse discourse structure into syntax or syntactic structure into morphology. Of course, there is some deliberate innovation in language (e.g., people consciously invent new words and phrases). But such deliberate innovations should be sharply distinguished from the unconscious operation of the basic learning and processing biases that have shaped the phonological, syntactic, and semantic regularities of language.

7.3. Language change "in vivo"

We have argued that language has evolved over time to be compatible with the human brain. However, it might be objected that it is not clear that languages become better adapted over time, given that they all seem capable of expressing a similar range of meanings (Sereno 1991). In fact, the idea that all languages are fundamentally equal and independent of their users – uniformitarianism – is widely adopted in linguistics, preventing many linguists from thinking about language evolution (Newmeyer 2003). Yet, much variation exists in how easy it is to use a given language to express a particular meaning, given the limitations of human learning and processing mechanisms.

The recent work on creolization in sign language provides a window onto how pressures towards increased expressivity interact with constraints on learning and processing "in vivo." In less than three decades, a sign language has emerged in Nicaragua, created by deaf children with little exposure to established languages. Senghas et al. (2004) compared signed expressions for complex motions produced by deaf signers of Nicaraguan Sign Language (NSL) with the gestures of hearing Spanish speakers. The results showed that the hearing individuals used a single simultaneous movement combining both manner and path of motion, whereas the deaf NSL signers tended to break the event into two consecutive signs: one for the path of motion and another for the manner. Moreover, this tendency was strongest for the signers who had learned NSL more recently, indicating that NSL has changed from using a holistic way of denoting motion events to a more sequential, compositional format.

Although such creolization may be considered as evidence of UG (e.g., Bickerton 1984; Pinker 1994), the results may be better construed in terms of cognitive constraints on cultural transmission. Indeed, computational simulations have demonstrated how iterated learning in cultural transmission can change a language starting as a collection of holistic form-meaning pairings into a more compositional format, in which sequences of forms are combined to produce meanings previously expressed holistically (see Kirby & Hurford 2002, for a review). Similarly, human experimentation operationalizing iterated learning within a new "cross-generational" paradigm – in which the output of one artificial-language learner is used as the input for subsequent "generations" of language learners – has shown that such learning biases over generations can change the structure of artificial languages from holistic mappings to a compositional format (Cornish 2006). This allows language to have increased expressivity, while being learnable from exposure to a finite set of form-meaning pairings. Thus, the change towards using sequential compositional forms to describe motion events in NSL can be viewed as a reflection of similar processes of learning and cultural transmission.

In a similar vein, the rapid emergence of a regular SOV (subject-object-verb) word order in Al-Sayyid Bedouin Sign Language (ABSL) (Sandler et al. 2005) can be interpreted as arising from constraints on learning and processing. ABSL has a longer history than NSL, going back some 70 years. The Al-Sayyid Bedouin group, located in the Negev desert region of southern Israel, forms an isolated community with a high incidence of congenital deafness. In contrast to NSL, which developed within a school environment, ABSL has evolved in a more natural setting and is recognized as the second language of the Al-Sayyid village. A key feature of ABSL is that is has developed a basic SOV word order within sentences (e.g., *boy apple eat*), with modifiers following heads (e.g., *apple red*). Although this type of word order is very common across the world (Dryer 1992), it is found neither in the local spoken Arabic dialect nor in Israeli Sign Language (ISL), suggesting that ABSL has developed these grammatical regularities de novo.

In a series of computational simulations, Christiansen and Devlin (1997) found that languages with consistent word order were easier to learn by a sequential learning device compared to inconsistent word orders. Thus, a language with a grammatical structure such as ABSL was easier to learn than one in which an SOV word order was combined with a modifier-head order within phrases. Similar results were obtained when human subjects were trained on artificial languages with either consistent or inconsistent word orders (Christiansen 2000; Reeder 2004). Further simulations have demonstrated how sequential learning biases can lead to the emergence of languages with regular word orders through cultural transmission – even when starting from a language with a completely random word order (Christiansen & Dale 2004; Reali & Christiansen, in press).

Differences in learnability are not confined to newly emerged languages but can also be observed in well-established languages. For example, Slobin and Bever (1982) found that when children learning English, Italian, Turkish, or Serbo-Croatian were asked to act out reversible transitive sentences, such as *the horse kicked the cow*, using familiar toy animals, language-specific differences in performance emerged. Turkish-speaking children performed very well already at 2 years of age, most likely because of the regular case-markings in this language, indicating who is doing what to whom. Young English- and Italian-speaking children initially performed slightly worse than the Turkish children but quickly caught up around 3 years of age, relying on the relatively consistent word order information available in these languages, with subjects preceding objects. The children acquiring Serbo-Croatian, on the other hand, had problems determining the meaning of the simple sentences, most likely because this language uses a combination of case-markings and word order to indicate agent and patient roles in a sentence. Crucially, only masculine and feminine nouns take on accusative or nominative markings and can occur in any order with respect to one another, but sentences with one or more unmarked neuter nouns are typically ordered as subject-verb-object. Of course, Serbo-Croatian children eventually catch up with the Turkish-, English-, and Italian-speaking children, but these results do show that some meanings are harder to learn and process in some languages compared to others, indicating differential fitness across languages (see Lupyan & Christiansen 2002, for corroborating computational simulations).

Within specific languages, substantial differences also exist between individual idiolects; for example, as demonstrated by the considerable differences in language comprehension abilities among cleaners, janitors, undergraduates, graduate students, and lecturers from the same British university (Dabrowska 1997). Even within the reasonably homogeneous group of college students, individual differences exist in sentence processing abilities because of underlying variations in learning and processing mechanisms combined with variations in exposure to language (for a review, see MacDonald & Christiansen 2002). Additional sources of variation are likely to come from the incorporation of linguistic innovations into the language. In this context, it has been suggested that innovations may primarily be due to adults (Bybee, in press), whereas constraints on children's acquisition of language may provide the strongest pressure towards regularization (e.g., Hudson Kam & Newport 2005). Thus, once we abandon linguistic uniformitarianism, it becomes clear that there is much variability for linguistic adaptation to work with.

In sum, we have argued that human language has been shaped by selectional pressure from thousands of generations of language learners and users. Linguistic variants that are easier to learn to understand and produce; variants that are more economical, expressive, and generally effective in communication, persuasion, and perhaps indicative of status and social group, will be favored. Just as with the multiple selectional pressures operative in biological evolution, the matrix of factors at work in driving the evolution of language is complex. Nonetheless, as we have seen, candidate pressures can be proposed (e.g., the pressure for incrementality, minimizing memory load, regularity, brevity, and so on); and regular patterns of language change that may be responses to those pressures can be identified (e.g., the processes of successive entrenchment, generalization, and erosion of structure evident in grammaticalization). Thus, the logical problem of language evolution that appears to confront attempts

to explain how a genetically specified linguistic endowment could become encoded, does not arise; it is not the brain that has somehow evolved to language, but the reverse.

8. Scope of the argument

In this target article, we have presented a theory of language evolution as shaped by the brain. From this perspective, the close fit between language learners and the structure of natural language that motivates many theorists to posit a language-specific biological endowment may instead arise from processes of adaptation operating on language itself. Moreover, we have argued that there are fundamental difficulties with postulating a language-specific biological endowment. It is implausible that such an endowment could evolve through adaptation (because the prior linguistic environments would be too diverse to give rise to universal principles). It is also unlikely that a language-specific endowment of any substantial complexity arose through non-adaptational genetic mechanisms, because the probability of a functional language system arising essentially by chance is vanishingly small. Instead, we have suggested that some apparently arbitrary aspects of language structure may arise from the interaction of a range of factors, from general constraints on learning, to impacts of semantic and pragmatic factors, and concomitant processes of grammaticalization and other aspects of language change. But, intriguingly, it also possible that many apparently arbitrary aspects of language can be explained by relatively natural cognitive constraints – and hence, that language may be rather less arbitrary than at first supposed (e.g., Bates & MacWhinney 1979; 1987; Bybee 2007; Elman 1999; Kirby 1999; Levinson 2000; O'Grady 2005; Tomasello 2003).

8.1. The logical problem of language evolution meets the logical problem of language acquisition

The present viewpoint has interesting theoretical implications concerning language acquisition. Children acquire the full complexity of natural language over a relatively short amount of time, from exposure to noisy and partial samples of language. The ability to develop complex linguistic abilities from what appears to be such poor input has led many to speak of the "logical" problem of language acquisition (e.g., Baker & McCarthy 1981; Hornstein & Lightfoot 1981). One solution to the problem is to assume that learners have some sort of biological "head start" in language acquisition – that their learning apparatus is precisely meshed with the structure of natural language. This viewpoint is, of course, consistent with theories according to which there is a genetically specified language organ, module, or instinct (e.g., Chomsky 1986; 1993; Crain 1991; Piattelli-Palmarini 1989; 1994; Pinker 1994; Pinker & Bloom 1990). But it is also consistent with the present view that languages have evolved to be learnable. According to this view, the mesh between language learning and language structure has occurred not because specialized biological machinery embodies the principles that govern natural languages (UG), but rather that the structure of language has evolved to fit with pre-linguistic learning and processing constraints.

If language has evolved to be learnable, then the problem of language acquisition may have been misanalyzed. Language acquisition is frequently viewed as a standard problem of induction (e.g., Gold 1967; Jain et al. 1999; Osherson et al. 1986; Pinker 1984; 1989), where there is a vast space of possible grammars that are consistent with the linguistic data to which the child is exposed. Accordingly, it is often readily concluded that the child must have innate knowledge of language structure to constrain the space of possible grammars to a manageable size. But, if language is viewed as having been shaped by the brain, then language learning is by no means a standard problem of induction. To give an analogy, according to the standard view of induction, the problem of language acquisition is like being in an unreasonable quiz show, where you have inadequate information but must somehow guess the "correct" answer. But according to the present view, by contrast, there is no externally given correct answer; instead, the task is simply to give the same answer as everybody else – because the structure of language will have adapted to conform to this most "popular" guess. This is a much easier problem: Whatever learning biases people have, so long as these biases are *shared* across individuals, learning should proceed successfully. Moreover, the viewpoint that children learn language using general-purpose cognitive mechanisms, rather than language-specific mechanisms, has also been advocated independently from a variety of different perspectives ranging from usage-based and functional accounts of language acquisition (e.g., Bates & MacWhinney 1979; 1987; MacWhinney 1999; Seidenberg 1997; Seidenberg & MacDonald 2001; Tomasello 2000a; 2000b; 2000c; 2003) to cultural transmission views of language evolution (e.g., Davidson 2003; Donald 1998; Ragir 2002; Schoenemann 1999), to neurobiological approaches to language (e.g., Arbib 2005; Deacon 1997; Elman et al. 1996) and formal language theory (Chater & Vitányi 2007).

From this perspective, the problem of language acquisition is very different from learning, say, some aspect of the physical world. In learning naïve physics, the constraints to be learned (e.g., how rigid bodies move, how fluids flow, and so on) are defined by processes outside the cognitive system. External processes define the "right" answers, to which learners must converge. But in language acquisition, the structure of the language to be learned is itself determined by the learning of generations of previous learners (see Zuidema 2003). Because learners have similar learning biases, this means that the first wild guesses that the learner makes about how some linguistic structure works are likely to be the right guesses. More generally, in language acquisition, the learner's biases, if shared by other learners, are likely to be helpful in acquiring the language – because the language has been shaped by processes of selection to conform with those biases. This also means that the problem of the poverty of the stimulus (e.g., Chomsky 1980; Crain 1991; Crain & Pietroski 2001) is reduced, because language has been shaped to be learnable from the kind of noisy and partial input available to young children. Thus, language acquisition is constrained by substantial biological constraints – but these constraints emerge from cognitive machinery that is not language-specific.

8.2. Natural selection for functional aspects of language?

It is important to emphasize what our arguments are *not* intended to show. In particular, we are not suggesting that biological adaptation is irrelevant for language. Indeed, it seems likely that a number of pre-adaptations for language might have occurred (see Hurford 2003, for a review), such as the ability to represent discrete symbols (Deacon 1997; Tomasello 2003), to reason about other minds (Malle 2002), to understand and share intentions (Tomasello 2003; Tomasello et al. 2005), and to perform pragmatic reasoning (Levinson 2000). There may also be a connection with the emergence of an exceptionally prolonged childhood (Locke & Bogin 2006). Similarly, biological adaptations might have led to improvements to the cognitive systems that support language, including increased working memory capacity (Gruber 2002), domain-general capacities for word learning (Bloom 2001), and complex hierarchical sequential learning abilities (Calvin 1994; Conway & Christiansen 2001; Greenfield 1991; Hauser et al. 2002), though these adaptations are likely to have been for improved cognitive skills rather than for language.

Some language-specific adaptations may nonetheless have occurred as well, but given our arguments above these would only be for functional features of language, and not the arbitrary features of UG. For example, changes to the human vocal tract may have resulted in more intelligible speech (Lieberman 1984; 1991; 2003 – though see also Hauser & Fitch 2003); selectional pressure for this functional adaptation might apply relatively independently of the particular language. Similarly, it remains possible that the Baldwin effect may be invoked to explain cognitive adaptations to language, provided that these adaptations are to functional aspects of language, rather than putatively arbitrary linguistic structures. For example, it has been suggested that there might be a specialized perception apparatus for speech (e.g., Vouloumanos & Werker 2007), or enhancement of the motor control system for articulation (e.g., Studdert-Kennedy & Goldstein 2003). But explaining innate adaptations even in these domains is likely to be difficult – because, if adaptation to language occurs at all, it is likely to occur not merely to functionally universal features (e.g., the fact that languages segment into words), but to specific cues for those features (e.g., for segmenting those words in the current linguistic environment, which differ dramatically across languages; Cutler et al. 1986; Otake et al. 1993). Hence, adaptationist explanations, even for functional aspects of language and language processing, should be treated with considerable caution.

8.3. Implications for the co-evolution of genes and culture

Our argument may, however, have applications beyond language. Many theorists have suggested that, just as there are specific genetic adaptations to language, there may also be specific genetic adaptations to other cultural domains. The arguments we have outlined against biological adaptationism in language evolution appear to apply equally to rule out putative co-evolution of the brain with any rapidly changing and highly varied aspect of human culture – from marriage practices and food sharing practices, to music and art, to folk theories of religion, science, or mathematics. We speculate that, in each case, the apparent fit between culture and the brain arises primarily because culture has been shaped to fit with our prior cognitive biases. Thus, by analogy with language, we suggest that nativist arguments across these domains might usefully be re-evaluated, from the perspective that culture may have adapted to cognition much more substantially than cognition has adapted to culture.

In summary, we have argued that the notion of UG is subject to a logical problem of language evolution, whether it is suggested to be the result of gradual biological adaptation or other non-adaptationist factors. Instead, we have proposed to explain the close fit between language and learners as arising from the fact that language is shaped by the brain, rather than the reverse.

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NOTES

1. For the purposes of exposition, we use the term "language genes" as shorthand for genes that may be involved in encoding a potential UG. By using this term, we do not mean to suggest that this relationship necessarily involves a one-to-one correspondence between individual genes and a specific aspect of language (or cognition).

2. Intermediate positions, which accord some role to both non-adaptationist and adaptationist mechanisms, are, of course, possible. Such intermediate viewpoints inherit the logical problems that we discuss in the following sections for both types of approach, in proportion to the relative contribution presumed to be associated with each. Moreover, we note that our arguments have equal force independent of whether one assumes that language has a vocal (e.g., Dunbar 2003) or manual-gesture (e.g., Corballis 2003) based origin.

3. Strictly, the appropriate measure is the more subtle *inclusive* fitness, which takes into account the reproductive potential not just of an organism, but also a weighted sum of the reproductive potentials of its kin, where the weighting is determined by the closeness of kinship (Hamilton 1964). Moreover, mere reproduction is only of value to the degree that one's offspring have a propensity to reproduce, and so down the generations.

4. In addition, Pinker and Bloom (1990) point out that it is often the case that natural selection has several (equally adaptive) alternatives to choose from to carry out a given function (e.g., both the invertebrate and the vertebrate eye support vision despite having significant architectural differences).

5. One prominent view is that language emerged within the last 100,000 to 200,000 years (e.g., Bickerton 2003). Hominid populations over this period, and before, appear to have undergone waves of spread; "modern languages derive mostly or completely from a single language spoken in East Africa around 100 kya ... it was the only language then existing that

survived and evolved with rapid differentiation and transformation" (Cavalli-Sforza & Feldman 2003, p. 273).

6. Human genome-wide scans have revealed evidence of recent positive selection for more than 250 genes (Voight et al. 2006), making it very likely that genetic adaptations for language would have continued in this scenario.

7. This setup closely resembles the one used by Hinton and Nowlan (1987) in their simulations of the Baldwin effect, and to which Pinker and Bloom (1990) refer in support of their adaptationist account of language evolution. The simulations are also similar in format to other models of language evolution (e.g., Briscoe 2003; Kirby & Hurford 1997; Nowak et al. 2001). Note, however, the reported simulations have a very different purpose from that of work on understanding historical language change from a UG perspective, for example, as involving successive changes in linguistic parameters (e.g., Baker 2001; Lightfoot 2000; Yang 2002).

8. Some recent theorists have proposed that a further pressure for language divergence between groups is the sociolinguistic tendency for groups to "badge" their in-group by difficult-to-fake linguistic idiosyncrasies (Baker 2003; Nettle & Dunbar 1997). Such pressures would increase the pace of language divergence, and thus exacerbate the problem of divergence for adaptationist theories of language evolution.

9. This type of phenomenon, where the genetically influenced behavior of an organism affects the environment to which those genes are adapting, is known as Baldwinian niche construction (Odling-Smee et al. 2003; Weber & Depew 2003).

10. Indeed, a population genetic study by Dediu and Ladd (2007) could, on the one hand, be taken as pointing to biological adaptations for a surface feature of phonology: the adoption of a single-tier phonological system relying only on phoneme-sequence information to differentiate between words, instead of a two-tier system incorporating both phonemes and tones (i.e., pitch contours). Specifically, two particular alleles of *ASPM* and *Microcephalin*, both related to brain development, were strongly associated with languages that incorporate a single-tier phonological system, even when controlling for geographical factors and common linguistic history. On the other hand, given that the relevant mutations would have had to occur independently several times, the causal explanation plausibly goes in the opposite direction, from genes to language. The two alleles may have been selected for other reasons relating to brain development; but once in place, they made it harder to acquire phonological systems involving tonal contrasts, which, in turn, allowed languages without tonal contrasts to evolve more readily. This perspective (also advocated by Dediu & Ladd 2007) dovetails with our suggestion that language is shaped by the brain, as discussed in sects. 5 to 7). However, either of these interpretations would argue against an adaptationist account of UG.

11. We have presented the argument in informal terms. A more rigorous argument is as follows. We can measure the amount of information embodied in Universal Grammar, U, over and above the information in pre-existing cognitive processes, C, by the length of the shortest code that will generate U from C. This is the conditional Kolmogorov complexity $K(U|C)$ (Li & Vitányi 1997). By the coding theorem of Kolmogorov complexity theory (Li & Vitányi 1997), the probability of randomly generating U from C is approximately $2^{-K(U|C)}$. Thus, if Universal Grammar has any substantial complexity, then it has a vanishingly small probability of being encountered by a random process, such as a non-adaptational mechanism.

12. Darwin may have had several reasons for pointing to these similarities. Given that comparative linguistics at the time was considered to be a model science on a par with geology and comparative anatomy, he may have used comparisons between linguistic change – which was thought to be well understood at that time – and species change to corroborate his theory of evolution (Alter 1998; Beer 1996). Darwin may also have used these language-species comparisons to support the notion that less "civilized" human societies spoke less civilized languages, because he believed that this was predicted by his theory of human evolution (Raddick 2000; 2002).

13. Chomsky has sometimes speculated that the primary role of language may be as a vehicle for thought, rather than communication (e.g., Chomsky 1980). This viewpoint has its puzzles: for example, the existence of anything other than semantic representations is difficult to understand, as it is these over which thought is defined; and the semantic representations in Chomsky's recent theorizing are, indeed, too underspecified to support inference, throwing the utility of even these representations into doubt.

14. Some studies purportedly indicate that the mechanisms involved in syntactic language are not the same as those involved in most sequential learning tasks (e.g., Friederici et al. 2006; Peña et al. 2002). However, the methods used in these studies have subsequently been shown to be fundamentally flawed (de Vries et al. [in press] and Onnis et al. [2005], respectively), thereby undermining their negative conclusions. Thus, the preponderance of the evidence suggests that sequential learning tasks tap into the mechanisms involved in language acquisition and processing.

15. The current knowledge regarding the *FOXP2* gene is consistent with the suggestion of a human pre-adaptation for sequential learning (Fisher 2006). *FOXP2* is highly conserved across species; but two amino acid changes have occurred after the split between humans and chimps, and these became fixed in the human population about 200,000 years ago (Enard et al. 2002). In humans, mutations to *FOXP2* result in severe speech and orofacial motor impairments (Lai et al. 2001; MacDermot et al. 2005). Studies of *FOXP2* expression in mice and imaging studies of an extended family pedigree with *FOXP2* mutations have provided evidence that this gene is important to neural development and function, including of the corticostriatal system (Lai et al. 2003). This system has been shown to be important for sequential (and other types of procedural) learning (Packard & Knowlton 2002). Crucially, preliminary findings from a mother and daughter with a translocation involving *FOXP2* indicate that they have problems with both language and sequential learning (Tomblin et al. 2004).

Open Peer Commentary

Language is shaped by the body

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Abstract: Sign languages provide direct evidence for the relation between human languages and the body that engenders them. We discuss the use of the hands to create symbols and the role of the body in sign language verb systems, especially in two quite recently developed sign languages, Israeli Sign Language and Al-Sayyid Bedouin Sign Language.

Christiansen & Chater (C&C) succinctly announce the major claim of their article in its title, which we will take the liberty of relettering (changing an *a* to an *i*) as: *language is shaped by the brain*. Our work on sign languages has led us to the broader but more easily verifiable claim that languages are shaped by the human body and its interaction with the world.

The greatest obstacle facing any claim about the relation between languages and the brain is the simple fact that we have precious little access to the inner workings of the human mind/brain and no direct access to the relation between the mind/brain and language. Indeed, C&C do not have much to say concretely about how the human mind/brain actually constrains languages (see sects. 6.2–6.3 of the target article).

But once we extend our purview beyond the brain and understand, as C&C do, that there are "other parts of our body involved in language" (sect. 6, para. 1), especially parts of the body that are visible to the naked eye, then we can literally see ways in which human languages are shaped by the body, not just the mind/brain part of it, and how they differ from the communication of other primates. Here students of sign languages have a great advantage over students of spoken languages, because sign languages, lacking sound, are *necessarily* fully visible. Concrete evidence for the relation between human languages and the body that engenders them comes from our own research on a number of sign languages, especially two quite recently developed sign languages, Israeli Sign Language (ISL) (Meir & Sandler 2008) and Al-Sayyid Bedouin Sign Language (ABSL) (Aronoff et al. 2008; Meir et al. 2007; Padden et al., in press; Sandler et al. 2005).

Following Wilson (2002), we assume that "The mind must be understood in the context of its relationship to a physical body that interacts with the world" (p. 625). We doubt anyone could quarrel with this statement, but it has broad consequences when taken as more than a slogan. We will discuss here two examples, both related to the iconicity afforded by visual language: the use of the hands to create symbols and the role of the body in sign language verb systems.

Sign languages use the hands to shape the often iconic symbols that enter into the linguistic system. No matter how young the language, and even in the absence of a community as in the case of home signers, people spontaneously use their hands and bodies to make symbols that represent other objects and actions – a cup, a flower, to see. This seemingly obvious fact reveals with startling clarity the essential difference between the language of humans and the communication systems of other primates. Nonhuman primates in the wild do use their hands and bodies to gesture, but the literature on their communication systems documents no case where a chimpanzee, bonobo, orangutan, or other primate relative uses its hands to represent a termite or a banana or any object *other* than its hands (Call & Tomasello 2007). The use of the body to represent the world symbolically in sign language provides compelling evidence for the view put forward by Deacon (1997) and others that symbolization is a more basic feature of language than arbitrariness (Sandler, in press). C&C "suggest that language does not involve any qualitatively different mechanisms compared to extant apes" (sect. 6.5, para. 3). Visual human languages call that suggestion into question.

The body interacts with the linguistic system separately from the hands in a complex way in the representation of the meanings of signs denoting states of affairs (verbs) in all sign languages that we know of (Meir et al. 2007). In what are called body-anchored verb signs, the signer's body consistently represents one argument of the verb, the subject, whereas the hands, moving in relation to the body, represent all other components of the event, including all other arguments. For example, the sign EAT is signed in all known sign languages by moving the hand towards the body (specifically, the mouth). The body represents the subject of the eating event. The hands represent the object being eaten and aspects of the event itself in EAT signs. This division of labor between body and hands is a clear indication of how the human body helps shape a grammatical system.

Common body-anchored signs in ISL are given in Table 1. These signs are of many different semantic types and the subject argument plays a different semantic role in each type; yet in all semantic types the body corresponds to the subject argument, the argument by which the event is predicted. Iconicity motivates the use of the body in this system, in which the emergent grammatical construct is the notion of subject.

The signer's body does not iconically stand for the subject in all verbs in all sign languages. For one, this particular iconic use of the body is typically limited to animate subjects. For another, most sign languages have another major category of verbs, usually called *agreement* verbs, in which the signer's body plays the role of grammatical first person (Padden 1988) and the use of the body to represent first person overrides or blocks the body-as-subject iconicity. Unlike the body-as-subject class, agreement verbs or "verbs of transfer" (Meir 2002), such as GIVE, SEND, SHOW, and TAKE, use reference points in the space around the body abstractly to represent syntactic arguments. See Aronoff et al. (2005) and Padden et al. (in press) for details.

Observing the emergence of new sign languages in real time allows us to take one step back in the development of language. These languages reveal strikingly the reliance on the body in expressing verbal notions. When they lack grammatical person marking and hence agreement verbs, all the transfer notions that are lexicalized as agreement verbs in established sign languages are lexicalized instead as body-anchored expressions and follow the body-as-subject pattern. We have documented this phenomenon in detail for ABSL and have shown how the emergence of the notion of grammatical first person in the diachronic development of ISL shifted the language from the body-as-subject pattern to the body-as-first-person pattern (Meir et al. 2007). The study of sign languages, especially

Table 1. *(Aronoff et al.) Common body-anchored signs in Israeli Sign Language*

Verb type	Bodily anchor	Subject role
Consumption: EAT, DRINK	Mouth Represents the mouth of the subject	Agent
Mental activity: THINK, KNOW, REMEMBER, LEARN	Temple or forehead Represents the site of the mental activity of the subject	Experiencer
Saying: SAY, ASK, ANSWER, TELL, EXPLAIN	Mouth Represents the mouth of the subject	Agent
Psychological state: HAPPY, LOVE, SUFFER, UPSET	Chest Corresponds to the symbolic location of emotions of the subject	Experiencer, patient
Change of physical state: BLUSH, GET-WELL, WAKE-UP	Face, Chest or eyes Represent the relevant part of the body of the subject	Patient

emerging sign languages, teaches us that our species relies on the human body in the creation and structuring of languages when it can.

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Adaptation to moving targets: Culture/gene coevolution, not either/or

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Abstract: We agree that much of language evolution is likely to be adaptation of languages to properties of the brain. However, the attempt to rule out the existence of language-specific adaptations a priori is misguided. In particular, the claim that adaptation to "moving targets" cannot occur is false. Instead, the details of gene-culture coevolution in language are an empirical matter.

We wholeheartedly agree with Christiansen & Chater's (C&C's) central point that much of language evolution is likely to be adaptation of languages, via cultural evolution, to leverage species-typical properties of the brain. They are right to point out that while many language universals have been taken to reflect properties of a genetically evolved Universal Grammar (UG), they could equally well be universal culturally evolved properties of languages. This possibility is insufficiently recognized and should be a major focus of study.

What we take issue with, however, are the ideas that this is an "either/or" issue and that it is possible to rule out a priori the existence of mechanisms that evolved specifically as a result of their effects on language acquisition. Instead, how genes and culture interact to produce language, and whether domain-specific mechanisms exist for language acquisition, are empirical matters.

The biggest problem with C&C's argument lies in their attempt to rule out the existence of UG a priori by proposing a "logical" problem of language evolution: namely, that adaptation to "moving targets" is impossible. Unfortunately, this claim is simply false. "Moving targets," in the sense of environments that vary over space and time, are the norm rather than the exception in biology. What matters for adaptation is not whether environments vary, but whether there are statistical regularities that natural selection could track. It is very likely that the world's languages do possess statistical regularities, some of which C&C point to.

In fact, it is not even necessary for the statistical regularities of the environment to be stable over time in order for adaptation to occur. One of the earliest ideas about this was Van Valen's (1973) "Red Queen" theory of antagonistic coevolution, in which different species, such as predator and prey, could be locked in ever-spiraling evolutionary arms races in which neither settle on a stable equilibrium. Nevertheless, these species can still evolve adaptations to the coevolving traits of the other, such as adaptations for fast running. Such coevolution is possible even when one party in the race can evolve "faster" than the other, as in host-parasite coevolution. This does not make impossible the existence of anti-parasite adaptations, such as the immune system (which C&C mention).

Perhaps the clearest and most relevant demonstration that genetic adaptation to culturally moving targets is possible can be found in the work of culture-gene coevolution theorists (Boyd & Richerson 1985; Richerson & Boyd 2005). The logic of these models is precisely that delineated by C&C: namely, that cultures vary substantially in time and space, such that precise genetic tracking of every cultural detail is impossible. Nevertheless, gene-culture coevolution models show that natural selection can favor genetically evolved mechanisms that facilitate the acquisition of local culture. Importantly, it is the *statistical* properties of cultural information that the genes track.

These models and associated empirical findings (Richerson & Boyd 2005) show that culture and genes can and do coevolve. Although it is certainly possible to make models in which genes are "locked in place" and culture evolves to them, or vice versa, it is very unlikely that this is empirically what happens. Culture exerts selection pressure on genes, and genes exert selection pressure on culture, simultaneously. This means that questions like "which came first, the genes or the culture?" are inherently problematic. The "circularity trap" of C&C (sect. 3.2.1) is a problem faced by people who think in an either/or way; it is not a problem faced by the evolutionary process itself.

We suggest that the proper way to think about the gene pool of our species – and about the pool of cultural phenomena such as language – are as statistical clouds spread across space and time, each adapting to the other. C&C are entirely right that the properties of languages adapt to the statistical properties of the mind to make it more learnable and more easily understood. But there is, contrary to C&C's claims, no a priori reason why genes that do the exact same thing would not also be selected for. Indeed, if such genes existed, they would inevitably be selectively favored. It is a mistake to think either that language leaps fully formed upon the stage, and genes evolve to it, or that a genetic apparatus for language evolves, and then language sprouts from it. The process is likely to have been coevolutionary, all the way up.

What we expect, on this view, is a mesh, or fit, between genetically evolved mental mechanisms and language. The kinds of mechanisms we expect are ones that fit well with the statistical properties of language, and the statistical properties of language should fit well with them; how much of this fit has evolved on either side is an empirical matter. Language acquisition mechanisms can be seen as "prepared learning" mechanisms that reduce the frame problems inherent in any kind of learning by expecting certain kinds of regularities, or statistically present properties, to exist in the local language. These might include properties like long-distance dependencies; lexical types such as nouns and verbs; word order as a disambiguating device; hierarchical structuring; mechanisms for marking conceptual features such as space, time, causation, agency, and mental states; and more.

We recognize that many of these features might be argued to emerge from interaction with mental mechanisms that are not language-specific, such as conceptual mechanisms (although the language/conceptual interface could be a language-specific adaptation). Moreover, C&C and others (including, perhaps, Chomsky) might argue that these features should not be regarded as part of "UG" because they are not "arbitrary" or "non-functional." However, we do not find it particularly useful to restrict UG to only "non-functional" features of language; among other things, it seems an odd way to carve up evolved structures. The important questions, for us, are twofold: (1) Do mechanisms exist that evolved because of their beneficial fitness effects on language acquisition? and (2) what are the computational properties of these mechanisms? We are happy to call these "UG," though they might end up being very different from

what Chomsky proposed. While we applaud C&C's efforts to draw attention to the culturally evolved properties of language that play a role in this evolutionary process, the authors have not convinced us that we should stop trying to look for the answers to questions (1) and (2).

Languages as evolving organisms – *The* solution to the logical problem of language evolution?

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Abstract: Christiansen & Chater (C&C) argue persuasively that Universal Grammar (UG) could not have arisen through evolutionary processes. I provide additional suggestions to strengthen the argument against UG evolution. Further, I suggest that C&C's solution to the logical problem of language evolution faces several problems. Widening the focus to mechanisms of general cognition and inclusion of animal communication research might overcome these problems.

Christiansen & Chater's (C&C's) arguments against sudden de novo evolution of a highly complex domain-specific structure (Chomskian Universal Grammar or UG) could be strengthened by the following suggestions. C&C underemphasize the fact that evolutionary change (e.g., mutations) occurs at the level of individual organisms. Therefore, we need to deal with more than the problem of the extremely low likelihood of non-adaptationist "arrival" of UG. In order to spread through the population, this language acquisition device (which would require language as input) would need to be passed on to the next generations; and it is difficult to imagine what selective advantage would occur. While a hypothetical lone organism who somehow macromutated an eye would have an advantage over her eyeless peers, a lone UG would be of questionable use in a community of nonlinguistic creatures.[1] Furthermore, evolution never plans ahead towards some future goal. Evolving a large, metabolically expensive brain because it could be "tweaked" into future UG (as proposed by Chomsky 1986; 2002) is almost certainly out of the question. Because evolutionary processes are restricted by existing structures and recruit not infrequently structures that originally evolved for some other purpose (excaptations; cf., Gould & Vrba 1982), we would expect UG to be similar to and not substantially different from other biological structures. These considerations strengthen C&C's arguments against the sudden occurrence of a monolithic Universal Grammar module (e.g., the "instantaneous Great Leap" defended by Chomsky as recently as 2006).

Concerning the problem of an adaptationist account of UG evolution, I suggest that C&C's arguments demonstrate convincingly why a monolithic UG with fundamentally arbitrarily (as opposed to functionally) determined constraints could not have evolved through natural selection. However, C&C have not shown that "specialized brain mechanisms specific to language acquisition" (sect. 1, para. 2) necessarily need to have the structure of UG. The exact nature of UG is controversial even among its proponents (e.g., Chomsky 1995; 2005b; 2006; Crain & Pietroski 2001; Fitch et al. 2005; Hauser et al. 2002; Jackendoff 2002; 2007; Lightfoot 1999) and critics point at the inadequacy of UG definitions (e.g., Cowie 1999; Deacon 1997; Pullum & Scholz 2002; Tomasello 2003). C&C repeatedly stress that their account is compatible with language-specific brain mechanisms that differ from UG, and it would be desirable to specify these mechanisms in some detail.

Having shown that a genetically determined brain structure like UG could not have evolved, C&C propose to shift the focus from brains to language itself. On their view (similar to proposals by Atkinson et al. 2008; Bichakjian 2002; Clark 1996; Deacon 1997; Kortlandt 2003; Ritt 2004; van Driem 2005), languages can be understood analogous to organisms that are shaped by brains and have evolved "to be easy to learn to produce and understand" (sect. 1, para. 3). This elegant solution to the logical problem of language evolution is not entirely unproblematic, and the following issues need to be addressed.

C&C claim that selection pressures working on language to adapt to humans are significantly stronger than pressures in the other direction because language can only survive if it is learnable, whereas humans can survive without language (sect. 5, para. 3). Survival is undoubtedly a necessary condition for natural selection, but it is not sufficient. Organisms need to reproduce to pass their traits on to the next generation. By analogy, a male peacock presumably can survive without a tail, but would he be able to attract a mate and reproduce? If language plays a role in mate selection (Burling 2005; Deacon 1997; Dunbar 2005; Franks & Rigby 2005; Johansson 2005; Miller 2000), then the selective pressures for language skills may be stronger than C&C allow.

C&C's suggestion that learnability is a constraint on languages sounds compelling for our modern, highly complex languages. But, assuming that the first (proto) languages were much simpler, the question arises why language did not remain much simpler. Further, as the example of language-specific performance differences in young Turkish, English, Italian, and Serbo-Croatian children (sect. 7.3, para. 6) shows, we find considerable differences in ease of learning and processing among existing languages. C&C's claim that languages are passed on as collection of interdependent features (sect. 5.2, para. 1) might explain why these differences continue to persist. But why and how did learnability differences arise in the first place? C&C suggest that "individual constructions consisting of words or combinations thereof are among the basic units of selection" (sect. 5.2, para. 2). Again, this already presupposes a fairly sophisticated language to be in place and sidesteps the important question of how more fundamental components of language evolved.

Finally, the intriguing computer simulations do not necessarily show that the algorithms used are not language-specific. It seems that in the examples cited, the problem space is limited by the initial conditions of the simulation; and therefore the results are compatible with UG (Bickerton 2003; Marcus 2001; Russell 2004). Further, the models seem to be restricted to some prespecified aspect of language, and it is not clear whether a complete language would require some domain-specific scaffolding (Marcus 1998; Russell 2004; Yang 2004).

Possibly some of these concerns can be addressed when we consider language evolution in the broader context of the evolution of other cognitive capacities. One interesting line of thought is the proposal that language comprehension, rather than production, was the driving force behind language evolution (Bickerton, 2003; Burling 2000; 2005; Origgi & Sperber 2000). Burling (2005) suggests that communication does not begin with a meaningful vocalization or gesture but with the interpretation of the behavior of another individual. An individual who can understand another's action even when no communication has been attempted gains an evolutionary significant advantage. This suggestion might direct us back at brain structures. Which structures underlie cognition in general and language specifically? It appears plausible that language is handled by several subsystems, which presumably also have non-linguistic functions (Deacon 1997; Fitch et al. 2005; Johansson 2005). It might be illuminating to include details emerging from research on animal communication (e.g., Arnold & Zuberbühler 2006; Doupe & Kuhl 1999; Fitch 2005; Gentner et al. 2006; Hauser et al. 2001; Orlov et al. 2000; Pepperberg 2000; Perruchet &

Rey 2005; Ramus et al. 2000; Terrace 2001; Zuberbühler 2005) in an account of language evolution.

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NOTE

1. Chomsky (2002) claims that language could have "enormous reproductive advantages" even if only possessed by a single person in the universe. Considering that this first language user would not have lived in a community of mute twentieth century intellectuals (but among hunter-gathers), this theory appears somewhat implausible.

Memes shape brains shape memes

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Abstract: Christiansen & Chater's (C&C's) arguments share with memetics the ideas that language is an evolving organism and that brain capacities shape language by influencing the fitness of memes, although memetics also claims that memes in turn shape brains. Their rejection of meme theory is based on falsely claiming that memes must be consciously selected by *sighted* watchmakers.

Christiansen & Chater (C&C) argue that features of the human brain have shaped language and that language itself is akin to an organism. This view is remarkably similar to that which emerges from memetics, and yet C&C summarily reject the views of meme-theorists. I shall explore the similarities and differences between memetics and C&C's view and argue that their rejection of memetics is misplaced.

In what sense is language an organism? C&C are slightly equivocal in answering this question. Although, in the target article's Abstract, they claim to "view language itself as a complex and interdependent 'organism,'" the quotation marks are a clue to their ambivalence, for later they claim that "Following Darwin (1900), we argue that it is useful metaphorically to view languages as 'organisms,'" (sect. 1, para. 3) and then repeat this *metaphorical* claim.

Darwin (1874) himself does not use the word "metaphor." He discusses parallels, homologies, and analogies, and writes of the struggle for life amongst words and grammatical forms, claiming that: "The survival and preservation of certain favoured words in the struggle for existence *is* natural selection" (Darwin 1874, p. 91; emphasis mine). My reading of Darwin is that he thought languages and organisms were similar because they both evolve by the processes of selection and modification with descent.

For memetics, too, the similarity is not metaphorical. The foundation of memetics (Dawkins 1976) is to apply universal Darwinism beyond biology. That is, memetics begins with the idea that information in culture is copied from person to person with variation and selection, and is, therefore, a replicator, just as genes are replicators. The term "meme" was coined to make this claim explicit; not primarily as an analogy with "gene," but as an example of another replicator operating on the same fundamental mechanisms.

Language is, on this view, a vast complex of memes, interconnected and co-evolved, and hence like a biological organism. This is not a metaphor; rather, biological organisms and languages are both complexes of replicators that are copied, protected, and work together for the same reason; their constituent replicators thrive better within the complex than they could outside it. In this sense, then, C&C propose a weaker version of the claims made by both Darwin and memetics.

Is language a parasite? C&C refer to it as a "beneficial parasite" (sect. 5.1, para. 4). I have, similarly, called it a parasite turned symbiont. Indeed, I have argued the same for all of culture (Blackmore 1999; 2001): Once imitation attained high enough fidelity, memes were let loose, and then spread and evolved, using human brains as their copying machinery. This happened, as Dennett (1995) emphasises, not for our benefit but for the benefit of the memes themselves. C&C point out that parasites and their hosts often co-adapt, with the parasite becoming less dangerous, but how dangerous was language when it began? I have argued that memes might have killed us off because of the burden they put on brain size, development, and energy use. If so, then we were lucky to pull through so that the brain and its parasite could begin to adapt to each other. They are now so well adapted that we cannot live without culture and language, and it is easy to make the mistake of thinking that language evolved for our benefit, rather than for its own.

C&C's main claim is that language did not shape the brain, but the reverse. They may have pushed this argument too far since much physical adaptation has clearly occurred – for example, in the restructuring of the larynx to improve articulation. Memetics implies that the effects work both ways, as memeplexes and biological organisms compete and co-evolve. Memes can shape genes; for example, memes with higher fidelity are more successful, and clearer articulation makes for higher fidelity, so that the spread of machinery capable of that articulation is then favoured (this is an example of "memetic drive," or the co-evolution of a replicator with its replicating machinery; Blackmore 1999; 2001). Also genes can shape memes, with memes that fit well to existing human brains having an advantage – as C&C describe.

Defending their view that biological adaptation to language is negligible, C&C cite the fact that when two species with different rates of adaptation enter a symbiotic relationship, the faster evolving one adapts to the slower one, but not the reverse. This may be so today, but we should not assume, from the speed of language change we observe now, that language memes always evolved much faster than genes. Indeed, evolutionary processes generally begin slowly and accelerate. Models of meme-gene co-evolution using increasing rates of memetic change have shown that a transition occurs at a certain relative rate of change, with gene evolution then effectively ceasing (Bull et al. 2000). It is therefore possible that early language memes did cause changes in human genes even though they no longer do so.

From these comparisons, it seems that C&C's views are, in important respects, similar to those of memetics. Why then do they so firmly reject the views "described by meme-theorists" (sect. 7.2, para. 6)?

I think the reason they give is spurious, and it has prevented them from seeing the potential value of memetics in explaining language evolution. They argue that memes are "created or selected by deliberate choice" (sect. 7.2, para. 6), whereas the constraints operating on linguistic structures are those "of which people have no conscious awareness" (sect. 7.2, para. 7). But this is not a defensible distinction. We humans may think that we are conscious, creative, "*sighted* watchmakers" (sect. 7.2, para. 6); but this arrogance is just part of the dualist illusion that we are not mere living machines but are inner selves with consciousness and free will (Blackmore 1999; Dennett 1991). One advantage of memetics is that it rejects this illusion and even tries to explain how it comes about. Humans are the product of two competing replicators: Biological creativity results from the evolutionary algorithm operating on one of those replicators, and human creativity from the same algorithm operating on the other (Blackmore 2007). Language is just one of the products of this blindly creative combination.

Prolonged plasticity: Necessary and sufficient for language-ready brains

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Abstract: Languages emerge in response to the negotiation of shared meaning in social groups, where transparency of grammar is necessitated by demands of communication with relative strangers needing to consult on a wide range of topics (Ragir 2002). This communal exchange is automated and stabilized through activity-dependent fine-tuning of information-specific neural connections during postnatal growth and social development.

Every species has a unique way of being in the world, and linguistic communication sets humans apart by providing a vehicle to convey information about physically and temporally displaced objects and events. Human languages utilize general-purpose learning mechanisms that yield a human product unique in the shear quantity and diversity of information. How is this possible?

We start by asking how the human brain gets its structure to the point of being language-ready. The answer to this may be simple. Early evolutionary changes in hominin developmental timing, occurring over three million years ago, produced a larger brain, relatively immature at birth, and open to postnatal restructuring. Changes in developmental timing to permit the birth of a large, skeletally immature infant accompanied a shift in posture and the anterior-posterior narrowing of the birth canal. Progressive prolongation of successive phases of fetal growth delayed skeletal ossification until after birth and resulted in a significant enlargement of the hominin brain relative to the postnatal growth of the body (Deacon 1997). Later divergence of brain from body size, occurring approximately one million years ago, appears to be linked to changes in diet and social organization (Aiello & Wheeler 1995; Milton 1999a; 1999b; Ragir 2001). A larger brain supported more sophisticated manipulations of the environment, fine-motor coordination, expanded short-term memory, and increased speed in information processing (Kien 1991). Such systemic evolutionary change provides an explanation for the emergence of capacities that make human brains language-ready.

The extended postnatal development of the human cortex affords information-specific pathways and modules as emergent features of neural organization. Dendritic and synaptic proliferation and pruning restructure the maturing brain in response to the environment and to the community of practices in which development is embedded (Adams & Cox 2002). In humans, passive as well as participatory experiences tune cortical pathways throughout an extended period of brain development and produce increasingly biased perceivers, more efficient learners, as well as behavioral complexity and innovation (Kuhl 2000). Statistical learning involves general learning mechanisms akin to classical conditioning, but some statistics are picked up more readily than others, with learning biases varying across primate species (Newport et al. 2004). Language learning fundamentally relies on memory of sequential and non-adjacent dependencies in the linear ordering of either auditory or visual elements. Auditory processing is especially well suited for tracking information distributed over time (Conway & Christiansen 2005), and humans show significant prenatal maturation and adaptations in the auditory system. Enhanced linear processing and Bayesian statistical learning mechanisms, however, are not language-specific, nor are they sufficient for language readiness.

Language is not merely a product of a language-ready brain; it is a cultural product of a community of practitioners. The crucial task is to identify the processes by which shared interpretations of the world are created among members of a community, as the co-construction of shared understanding forms the basis for any exchange of information. Co-constructed activities generate shared understandings of the relationships between vocal, manual, or body gestures that drop out and take meaning from ongoing events. Through social interaction, children learn the repetitive activity patterns of their community of which vocalizations form an integral part (Nelson 2006). As an accompaniment to shared activity, vocalization is public, reflexive, and separates out of ongoing events to stand for all or part of the activity (Carpendale & Lewis 2004). Each learner engages with the language that exists in the community to the extent that he or she is developmentally and socially capable (Ninio 2006; Wray & Grace 2005). One of the challenges for developmental theorists is to identify the entry points to this vast web of cultural knowledge, and how the child's activity within and representations of this cultural system become elaborated over time. Language acquisition requires a constant give-and-take between the child and others about the meaning of communicative exchanges in social interactions (Taylor 1997). Figure 1 adapts C&C's Figure 3b to include the dynamic negotiation of shared meaning occurring in the community.

Christiansen & Chater (C&C) propose the analogy of language as a "beneficial parasite" (sect. 5.1) symbiotic to the human brain in so far as the systematicity of language is a function of how brains learn. In our opinion, this analogy misleads and ignores the homology between language and all other human inventions. Dynamically negotiated cultural systems such as tool manufacture, music, and play are similarly constrained by body schema and the construction of experience-dependent neural networks, and arise from the needs of users to coordinate their perspectives and

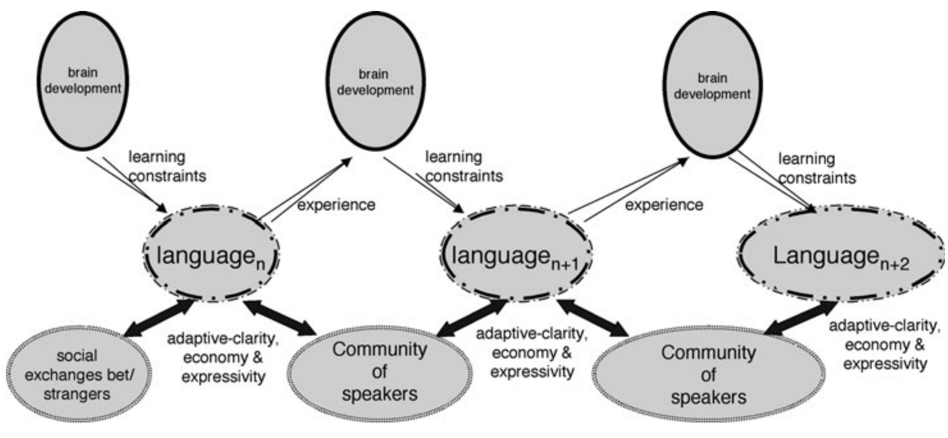


Figure 1 (Brooks & Ragir). Negotiation and Constraint in Language Formation.

goals. Complexity in any cultural system emerges over a historical time frame; hierarchy and systematicity are emergent properties, contingent on critical numbers of communicators and topics (Kirby 1999). As work on the emergence of indigenous sign languages demonstrates, languages are not elaborated without a community of signers (Kegl et al. 1999; Ragir 2002; Senghas et al. 2004). As a community increases in size, and members lack intimate knowledge of one another, "rules" emerge from the competing pressures of efficiency, clarity, and expressiveness, and streamline the exchanges of information to reduce cognitive effort (Kirby 1999; Ragir 2002; Wray & Grace 2005). In any cultural system, arbitrary categories are difficult to keep track of, and overlapping, redundant patterns of expression are favored. Languages increase in semantic and grammatical complexity as needed within developmental and historical time-scales. Such systematization is a universal property of culturally negotiated systems, rather than a property of the brain (Bak 1996). Similarly, pragmatic principles are not simply constraints, analogous to perceptual-motor or cognitive capacities, but reflect social practices involved in coordinating perspectives for effective communication (Clark 1996a; Hilton 1995). While C&C suggest that the possession of language might have fundamentally changed the patterns of collective problem solving, we would argue that collective problem solving led to the co-construction of language.

Finally, C&C make an unnecessary capitulation to the speculations of evolutionary psychology in their concession that cognitive pre-adaptations probably evolved through natural selection before language emerged. We suggest that changes in habitat, diet, and social organization co-evolved with the increased nutritional demands of encephalization and the socialization of dependent offspring during an extended childhood. Just as human languages emerged out of the exchanges of information within human societies, cooperation, joint attention, theory of mind, symbolic thought, and pragmatic reasoning are just as likely to have been products of dynamic negotiations within communities.

Convergent cultural evolution may explain linguistic universals

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Abstract: Christiansen & Chater's (C&C's) argument rests on an assumption that convergent cultural evolution can produce similar (complex) behaviours in isolated populations. In this commentary, I describe how experiments recently carried out by Caldwell and colleagues can contribute to the understanding of such phenomena.

Christiansen & Chater (C&C) make an excellent argument, both against the plausibility of an innate language-specific Universal Grammar (UG) and for the likelihood of the cultural evolution of language in response to selective pressures associated with use and learnability. In terms of challenging the concept of an innate UG, one of their strongest arguments concerns the implausibility of the independent evolution of highly similar UGs within isolated populations, and also the improbability that a common ancestor UG could be maintained in its original form should a previously unified population split and disperse.

C&C's argument that apparent linguistic universals are therefore attributable to the cultural evolution of language, as opposed to biological evolution of an innately specified UG, hence depends on a notion of convergent cultural evolution. In biological evolution, convergent evolution refers to a process by which species that are only distantly related independently evolve analogous adaptations in response to similar environmental pressures. Convergent cultural evolution therefore refers to situations in which different populations independently develop similar socially transmitted behaviours despite different ancestral histories. In C&C's account, similarities in languages will arise due to similarities in human brains, thereby imposing similar selective pressures on the process of cultural evolution. In other accounts (e.g., Deacon 1997; 2003a; 2003b), similarities may also emerge as a result of functional constraints associated with communication that are, in a sense, external to brains (Deacon [2003a], for example, has suggested that many of the features common to human languages might also be found in any symbolic communication system, such as one used by an alien species from another planet). On either of these accounts, however, it is essentially convergent cultural evolution which is producing the observed uniformities in behaviour across populations.

In order to fully develop and support such views, it would be useful to understand more about how such cultural convergence is likely to operate. Although there are many cases that can be, with hindsight, attributed to convergent cultural evolution (e.g., the independent development of writing systems [Mesoudi et al. 2004]; or cross-cultural similarities in colour terms [Deacon 1997]), ideally we would have access to complete datasets to track the relevant behavioural histories, and would be able to control likely sources of variation. Mesoudi (e.g., Mesoudi 2007; Mesoudi & O'Brien 2008) has argued that, for just such reasons, experimental approaches are particularly valuable in the study of culture.

In our experiments (e.g., Caldwell & Millen 2008) we have been making use of "microsociety" (e.g., Baum et al. 2004), or "microculture" (e.g., Jacobs & Campbell 1961), methods in order to allow us to study cultural phenomena under controlled laboratory conditions over short time periods. Generational succession is simulated within small test groups of participants by periodically removing the longest-standing member of the group and replacing them with a naive individual. While in the test group, participants are required to complete simple tasks using everyday materials, with clear goals. In one of our procedures, participants were instructed to build a paper aeroplane which flew as far as possible, and in the other, they were instructed to construct a tower from spaghetti and modelling clay which was as tall as possible. We have shown that, in both cases, information accumulated within the groups such that later generations produced designs which were more successful than earlier ones.

However, more relevant from the point of view of the target article is that we also have evidence of convergent cultural evolution. For each of our tasks we ran ten chains each of ten participants, and different chains had no contact with one another (simulating isolated cultures). Photographs of the objects produced by each participant were rated for similarity. Although there was clear evidence of cultural variation (designs were rated as being more similar to others from the same chain, compared with those from different chains), there was also evidence of convergence, since designs further down the chains were more similar to one another compared with those at the start of the chains. So, the tenth designs from each of the ten chains were rated as being more similar to one another, compared with the first designs from each of the chains. Thus, we have been able to demonstrate experimentally that over generations of cultural transmission, behaviours can become increasingly similar when shaped by similar selection pressures (in our case, the goal measures).

Our experiments are admittedly highly simplified models of cultural transmission, and the goals involved in our tasks are very far removed from the communicative functions performed by language. C&C also draw particular attention to the fact that language evolution may be a special case in terms of cultural evolution, in that users are not consciously designing their behaviours (although see Mesoudi 2008 for a different view). All the same, we believe our results are illustrative of general

phenomena which we suspect to be at work across a variety of contexts involving cultural transmission. Importantly, our experiments clearly show that complex adaptive behaviours can arise through cultural transmission, and that these behaviours, shaped by similar selection pressures, can show effects of convergence across isolated populations.

Brain and behavior: Which way does the shaping go?

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Abstract: Evolutionary contingencies select organisms based on what they can do; brains and other evolved structures serve their behavior. Arguments that brains drive language structure get the direction wrong; with functional issues unacknowledged, interactions between central structures and periphery are overlooked. Evidence supports a peripherally driven central organization. If language modules develop like other brain compartments, then environmental consistencies can engender both structural and functional language units (e.g., the different phonemic, semantic, and grammatical structures of different languages).

If evolutionary contingencies select organisms based on what they can do, then brains and other evolved structures serve behavior. Behavior is an essential starting place for understanding those structures. But Christiansen & Chater (C&C), starting from a different direction, recommend the brain as starting place; they acknowledge an environmental role in the shaping of languages by language users, but offer precious little about details.

Central to C&C's position is Universal Grammar (UG), which resides in the brain. In their case, UG's particulars arise from patterns of language use rather than from innate sources, whether evolved or originating in some other way. We are not told how it got there, although C&C make a case for its emergence through interactions among language learners and users (perhaps a step backwards from Pinker & Bloom's [1990] BBS argument for language as an evolved system, but maybe a step toward acknowledging memetic roots in the evolution of particular languages). Neither are we told much about the properties of UG, which, as C&C acknowledge, have been a moving target since UG was initially proposed (e.g., Colapinto 2007).

However UG is defined, and whatever its locus, either inside the head or extending into the language communities that according to C&C have engendered it, its import is primarily structural. It bears little on semantics (it doesn't really matter what people say as long as they do so grammatically) or on sentence function (the properties of imperatives don't really depend on what people do upon hearing them). In fact, probably C&C would not regard questions about function as even within the purview of linguistics: If questions are not about grammar, they are not about language (see also Jackendoff's [2003] BBS treatment, which dealt with structural relations among syntactic, semantic, and phonetic systems but attended little to function).

The trouble is not just that such accounts leave out too many phenomena that should be of interest, but also that such limitations on the boundaries of inquiry may blind us to the interdependence of structure and function (A. C. Catania 2000). It is as if we were interested in locomotion but looked only at particular interactions among muscles, examining coordinations as some muscles flexed while opposing ones relaxed and studying how movements at one joint depended on those at others. We could generate a grammar of locomotion, say, for the horse; and from it we might derive a systematic account of possible and impossible gaits. We might categorize different gaits (trots, canters, gallops), and perhaps could show that some not seen in nature (the rack) are teachable but others are not. Maybe we could go even further and show that some coordinations entering into our grammar of locomotion are pre-wired in the spinal cord (a Universal Grammar for Horses: UGH). But this would tell us nothing about where or when a horse might run, or with which gait, or whether in running it is following other horses or fleeing predators. The details of its locomotion, and thus the systems supporting it (e.g., muscles, tendons, bones, brain), evolved in the service of successful running.

These limitations apply even if we look only at horse locomotion. Suppose, however, that we sought a more general theory, applicable to all mammalian quadripeds or, to make it really universal, to all organisms. How should we adapt our grammar to the flippers or fins of aquatic animals? How about birds, and not just when they fly, but also when they walk or swim? And how about insects and arthropods, not to mention the vestigial limbs of snakes and our own bipedal walking? We can hardly deal with such differences without considering evolutionary contingencies, and the essence of such contingencies lies in the functions of locomotion. Were UGH adherents unwilling to extend UGH to these marvelous diversities, we might be sorely tempted to accuse them of a lack of imagination.

I argue, then, that C&C's position on language is comparable to the UGH grammarian's on locomotion, with different language communities substituting for our various locomoting species. In both cases, far too much is left out. Why so little about how particular vocabularies are acquired, or how speech interacts with other behavior? How might current environments shape linguistic units within an individual lifetime?

Space precludes an account of what we know about functional properties of language and ways in which contingencies shape the behavior of speakers (see A. C. Catania 2003a; 2006). But let us at least consider how the periphery might sculpt language units. Developing nervous systems divide into functional regions sometimes called compartments; of particular relevance is how boundaries form between them (e.g., Irvine & Rauskolb 2001; Kiecker & Lumsden 2005). For example, cortical tactile receptor areas in primates include boundaries between the projection areas for different fingers that can be visualized with appropriate stains. The boundaries may arise because adjacent cells on one finger are likely to be stimulated at the same time, whereas those on a neighboring finger, though projected close by on the cortex, are likely often to be stimulated separately. The number of compartments is determined during development by peripheral units (e.g., the separate rays in the nose of the star-nosed mole: K. C. Catania & Kaas 1997).

A long-standing puzzle is how exposure to linguistic environments can lead to discrimination among native phonetic units well before children begin to produce them. If projections from basilar membrane to auditory cortex have spatial properties that might correspond to phonetic boundaries, then a similar system could lead to separate *b* and *p* areas for children in an English-speaking environment and not for those in an Arabic-speaking environment, which lacks separate *b* and *p* consonant classes. The categorical perception emerging from such a process would certainly depend on the brain but could hardly be understood without a role for acoustic environments. Language units so created could then interact with the environment through other functional contingencies. And if it worked so for phonetic structure, should we not extend the account to syntactic and semantic structures?

If neural organization so depends on peripheral and environmental organization, plausible arguments follow about how environmental consistencies can sculpt boundaries and compartments corresponding to verbal units and to both structural and functional components of language (e.g., phonetic structure within given language communities, particular vocabularies, and perhaps even functional grammatical distinctions such as imperative versus declarative).

I have focused especially on directionality: To what extent do anatomies, environments and behavior drive or become driven by each other, and how might our understanding of language be illuminated by taking their interactions into account? In arguing that C&C have neglected the direction from behavior to brain, I have not maintained that things cannot go both ways.

Really, I do not doubt that the brain is important. But the brain is an adaptable organ, and it variously accommodates itself to the body and the broader environment within which it finds itself. When the brain is damaged in a stroke, one part of rehabilitation these days is to get the affected peripheral parts moving again: If the left arm is partially paralyzed, get the patient to use it by immobilizing the right arm. It is sometimes said that this treatment uses changes in behavior to change the brain, but the target of the therapy is, after all, the recovery of the behavior.

Both directions, from behavior to brain and from brain to behavior, are obviously significant. It would be astonishing to think that the same reciprocity does not exist for language. To the extent that C&C argue otherwise, they fail to make their case. It is premature to give up on evolutionary contingencies (A. C. Catania 2001; 2003b); C&C can escape from a creationism in which language emerges from the brain, not a fully grown Venus but ready to be shaped into one, by taking into account how environments shape the brain.

Time on our hands: How gesture and the understanding of the past and future helped shape language

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Abstract: Recognising that signed languages are true languages adds to the variety of forms that languages can take. Such recognition also allows one to differentiate those aspects of language that depend on the medium (voiced or signed) from those that depend on more cognitive aspects. At least some aspects of language, such as symbolic representation, time markers, and generativity, may derive from the communication of the products of mental time travel, and from the sharing of remembered past and planned future episodes.

The notion of Universal Grammar (UG) is, or was, one of the most uneasy concepts in cognitive science. Not only has it ultimately failed to capture the enormous diversity of human language, but it also lacks credibility in evolutionary terms. Chomsky himself was driven to conclude that language could not be the outcome of natural selection, once declaring that "It would be a serious error to suppose that all properties, or the interesting structures that evolved, can be 'explained' in terms of natural selection" (Chomsky 1975, p. 59) – although he seems more recently to have had something of a change of heart (see Hauser et al. 2002). Christiansen & Chater (C&C) have done cognitive and evolutionary science an enormous service by pointing out the deficiencies of UG as a plausible concept, and giving breathing space to alternative, more naturalistic approaches.

I think, though, that their title is slightly misleading, as the brain is scarcely mentioned in their article. Rather, they make a good case for supposing that language is shaped by human knowledge, learning capacities, and culture, and is not some encapsulated system with its own rules. I would like simply to add some points that I think support their general position.

In an endnote, C&C suggest that their arguments have equal force regardless of whether language has its origins in vocalizations or in manual gestures (see Note 2 of the target article). It may be useful, though, to note that even present-day language can be either spoken or signed (Emmorey 2002), and is indeed typically a combination of both (McNeill 1992). C&C do appeal to evidence from newly emerging sign languages to support their arguments concerning processes of grammaticalization, but for the most part they equate language with speech. Adding signed languages and manual gestures provides a better appreciation of the full repertoire of human language, and can help differentiate those aspects of language that depend on the particular medium of expression from those that may reflect more cognitive aspects. Thus, in section 6.2, C&C note that "The seriality of vocal output ... forces a sequential construction of messages" – the transformation known as *linearization*. But this constraint is much less severe in the case of signed languages, which can allow some degree of parallel output, and spatial mapping.

The notion of a "mother tongue" originating some 100,000 to 200,000 years ago, and giving rise to present-day languages, also presumably applies to speech rather than to language itself. Present-day signed languages appear to have emerged independently of any spoken language. One example, mentioned by C&C, is Al-Sayyid Bedouin Sign Language (ABSL), which bears little relation to the other languages, spoken or signed, of the region (Sandler et al. 2005). I agree with C&C that this is not proof of an innate UG, but, equally, it cannot be construed as a descendent of any mother tongue. It also allows one to speculate that language itself goes back much further than the last 100,000 or 200,000 years ago, as proposed by Bickerton (2003) or Cavalli-Sforza and Feldman (2003). I see no reason why our large-brained forebears of 500,000 or 1,000,000 years ago could not have invented something like ABSL, though perhaps with some vocal accompaniment (Armstrong & Wilcox 2007; Corballis 2004; 2006).

One cognitive domain that may have influenced, and perhaps even shaped, the evolution of language is mental time travel – the ability to mentally relive events in the past (episodic memory) or imagine events in the future. This is arguably uniquely human (Suddendorf & Corballis 1997; 2007). Language seems almost tailor-made to allow individuals to share past experiences and future plans, with adaptive consequences (Corballis & Suddendorf 2007). The features of language that may derive from mental time travel, or that perhaps co-evolved with it, include the following:

1. Symbolic representations allowing reference to actions, actors, objects, and so forth, that were part of episodes at times and places other than the present.
2. Ways of referring to different points in time, including past, present and future, and for making other temporal distinctions, such as action completed versus action ongoing. Languages have different ways of doing this. Many languages, such as English, have systems of tense, whereas others, like Chinese, have no tense but use other kinds of time markers (Lin 2005). Culture may play a hand here; thus, the Pirahã seem merely to distinguish between events that are in the present from those that are not (Everett 2005).
3. Generativity. The imagining of future events includes the generation of different possible scenarios – and even episodic memory appears to involve an element of construction – to the point that "memories" are often false (e.g., Roediger & McDermott 1995). Closely related to mental time travel, I suspect, is fiction – the deliberate construction of stories that are not based on fact, but that nonetheless serve as surrogates for experience. Correspondingly, the generativity of human language is perhaps its most distinctive property.

If we marry the emergence of mental time travel with a language that was based on manual gestures, we can look nostalgically back to an era when we had time on our hands.

A biological infrastructure for communication underlies the cultural evolution of languages

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Abstract: Universal Grammar (UG) is indeed evolutionarily implausible. But if languages are just "adapted" to a large primate brain, it is hard to see why other primates do not have complex languages. The answer is that humans have evolved a specialized and uniquely human cognitive architecture, whose main function is to compute mappings between arbitrary signals and communicative intentions. This underlies the development of language in the human species.

Christiansen & Chater (C&C) correctly pinpoint a number of serious problems for a detailed, innate Universal Grammar (UG). Language turns out to be, after all, just a part of culture, participating in all the associated processes of twin-track co-evolution (Durham 1991), including the cognitive filtering of possible cultural products (Levinson & Jaisson 2006). Recent work shows just how grammatical features are subject to cultural evolutionary processes (Dunn et al. 2005).

However, we should avoid throwing out the proverbial baby with the bathwater: There is a biological basis for language in two areas at least. First, the input/output systems (auditory specializations, vocal anatomy) clearly involve biological evolution (Lieberman & Blumstein 1988). Second – and this is the subject of this commentary – there is an underlying cognitive infrastructure for human communication. To see this, consider the conundrum the target article authors now face. Most properties of the human brain are just enlarged versions of ancient structures shared throughout the primate order and beyond. Our nearest cousins, the two chimp species, are highly intelligent animals that can master most human tasks not mediated by language (Tomasello & Call 1997). So how come they do not have the kinds of elaborate communicative systems we call language?

The answer to this, we think, is that humans have inherited a cognitive infrastructure for communication that probably goes way back in the hominin line. This infrastructure is perhaps correlated with the increasing encephalization characteristic of hominin evolution, the characteristic that makes language possible.

We agree with C&C that these prerequisites for the emergence of language are not to be found in the structural properties of languages themselves. However, contra C&C, we believe that they cannot be found in the "accidental" properties of our general cognitive abilities either. Instead, we propose that humans have developed what we would quite generally term *communicative intelligence* (see Enfield & Levinson 2006). The main function of this specific type of intelligence is to encode and decode the communicative intentions behind any type of potentially communicative behavior, linguistic, nonverbal, or otherwise (e.g., gestures). Without such specialized structures, the speed and flexibility with which language (in multiple modalities) is used, learned, and changed, even within one generation, would not be possible.

Empirical evidence for our assumption comes from the following findings.

A. Even for adults who have fully mastered their native language(s), linguistic signals are abundantly ambiguous and underdetermined. The idea that thoughts are encoded into linguistic utterances, sent to a receiver through a medium such as voice or hands, and then are decoded back into the original thought – a naive idea that has been endorsed by many scientists, from Saussure to Shannon – can and has repeatedly been shown to be false (see Levinson 1983; 2000 for multitudes of examples and further references). There is therefore a fundamental mismatch between coded content and communicative import, and the gap is filled by reasoning about likely communicative intentions. The upshot here is that it is not language that enables us to communicate; rather, it is our communicative skills that enabled us to use language.

B. Many systematic "errors" that at first sight appear to be cognitive "limitations" of humans, are in fact highly functional in the context of human communication (Levinson 1995). Key among these is the tendency to attribute intentional design to natural objects, events, and processes, with all the attendant irrationalities of magic, superstition, religion, and gambling. But that tendency is exactly what is needed to understand complex communicative signals, where one has to work out the communicative intention behind them. The ability to "read" these signals appears to carry with it the overdeterminative interpretations of events that are characteristic of human reasoning (Tversky & Kahneman 1977).

C. Languages are independent of sensory modality, as shown in human haptic or sign languages (Emmorey 2002). These gestural languages can develop from scratch in cultures (Senghas & Coppola 2001) and even in families (Goldin-Meadow 2005). Comparing this rapid development of systems of form-meaning mappings with the enormous efforts involved in getting intelligent species of mammals to communicate using language (see, e.g., Herman et al. 1984; Savage-Rumbaugh 1984) provides strong support for the existence of innate communicative capacities in humans.

D. Human communication is amazingly flexible and effective even in the absence of a shared, conventional language. Several recent studies have shown that participants who are confronted with the need to communicate, but have only limited and previously unknown channels at their disposal, are able to develop new signal-to-meaning mappings on the fly, within a matter of minutes (De Ruiter et al. 2007; Galantucci 2005). De Ruiter et al. have shown that in performing these types of tasks, both senders and receivers of signals show activation in the same small and well-defined brain region, suggesting that senders and receivers *simulate* one another's inferential processes in order to achieve successful communication.

The evolution of language becomes much less mysterious when this communicative or pragmatic infrastructure is given its proper place. This cognitive infrastructure has evolved slowly over the six million years of separation from our nearest primate relatives, is shared by all humans, and is invariant across all human languages (Levinson 2006). Languages are not adapted to just any primate brain – they are created and filtered by brains that are biologically endowed with communicative intelligence. Together with the vocal/auditory apparatus, this cognitive adaptation for communication makes possible the cultural evolution of spoken languages.

Why is language well designed for communication?

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Abstract: Selection through iterated learning explains no more than other non-functional accounts, such as Universal Grammar (UG), why language is so well designed for communicative efficiency. It does not predict several distinctive features of language, such as central

embedding, large lexicons, or the lack of iconicity, which seem to serve communication purposes at the expense of learnability.

Christiansen & Chater (C&C) rightfully observe that communicatively arbitrary principles, such as UG, are unable to explain why language is adequate for communication. The same criticism can be addressed, however, to their own account. If the main driving force that led to language emergence is learnability rather than communicative efficiency, language should be locally optimal for the former and *not* for the latter. Evidence suggests that, in several respects, the exact opposite is the case.

What would language be like if, as C&C claim, the cultural selection of learnable languages were "stronger" than the biological selection of brains designed for efficient communication? If language can compare with a "viral" entity that gets selected for its ability to resist vertical cultural transmission, we predict, for instance, *iconic signifiers*, especially gestures, to win the contest. Yet, although analogue resemblance makes learning almost trivial, linguistic evolution shows that non-iconic signifiers tend to prevail, even in sign languages.

The "viral" theory of language does not explain the *size of lexicons* either. Ideally, an expressive code is easiest to learn, and resists iterated transmission best, if words are limited in number and have separate and unambiguous meanings. Yet, real vocabularies include tens of thousands of words, massive near synonymy, and many rare unpredictable word combinations (Briscoe 2006). Such evidence suggests that there may be some "viral" cause for the existence of plethoric lexicons, but its action is opposite to what is expected from selection for learning efficiency.

Language, as mainly shaped by selection through repeated learning, is supposed to mirror the general human induction bias. Efficient induction systems (Solomonoff 1978), including human learning (Chater 1999) and analogy making (Cornuéjols 1996), are guided by a *complexity minimization principle*. If languages were the bare expression of a simplicity-based induction device looping on itself, we should expect the complexity of languages to converge to a minimal amount. A similar claim is that general-purpose learning devices, except in rote learning mode, produce only "good shapes" (Gestalten) – that is, structures that are left invariant by operations forming an algebraic group (Dessalles 1998a). Language has not, so far, been described as involving good shapes. For instance, syntactic structures, contrary to many other aspects of cognition, cannot be induced as invariants of transformation groups (Piattelli-Palmarini 1979) and seem to thwart general inductive processes (Piattelli-Palmarini 1989).

In a bio-functional account of language emergence, learnability puts limits on what is admissible, but is subordinate to communicative functions. The two main proximal functions of language in our species, as revealed by the observation of spontaneous language behavior, are *conversational narratives* and *argumentative discussion* (Bruner 1986; Dessalles 2007). From a bio-functional perspective, iconicity is dispensable if the problem is to express predicates for argumentative purposes (Dessalles 2007). Lexical proliferation is predicted if the problem is to signal unexpectedness in narratives and to express nuances in argumentative discussion (Dessalles 2007). And language-specific learning bias is expected if early language performance makes a biological difference. Let us consider a fourth example to show that functional aspects of language could evolve at the expense of learnability.

Non-functional accounts of language, including cultural selection through iterated learning, do not account for the existence of *central embedding* (the fact that any branch may grow in a syntactic tree), a feature present in virtually all languages. Recursive syntax has been shown to emerge through iterated learning, but only when individuals already have the built-in ability to use recursive grammars to parse linguistic input (e.g., Kirby 2002). A bio-functional approach to language provides an explanation for the presence of central embedding in language. As soon as the cognitive ability to form predicates is available, possibly for argumentative purposes (Dessalles 2007), predicates can be recruited to determine the arguments of other predicates. This technique is implemented in computer languages such as Prolog. To express "Mary hit Paul" for listeners who do not know Mary, the speaker may use "Mary ate with us yesterday" to determine the first argument of "hit." Prolog achieves this through explicit variable sharing, whereas human languages connect phrases for the same purpose: "The girl who ate with us yesterday hit Paul" (Dessalles 2007).

Predicates P_{1i} can therefore be used to determine arguments in a given predicate P_1; but each P_{1i} may require further predicates P_{1ij} to determine its own arguments. This possibility leads to recursive syntactic processing that produces central embedded phrase structures. Models that ignore functions such as predicate argument determination cannot account for the necessity of embedded phrase processing. They merely postulate it, either as a consequence of some fortuitous genetic accident (Chomsky 1975) or deduced from a general cognitive ability to perform recursive parsing (Kirby 2002). But then, the adequacy to the function is left unexplained as well. No single genetic accident and no selection through repeated learning can predict that phrase embedding will efficiently fulfill predicate argument determination. Only a bio-functional approach that derives the existence of phrase embedding from its function can hope to explain why recursive processing came to exist *and* why it is locally optimal for that function.

From a phylogenetic perspective, we may wonder why, if human languages have been selected to be easily learned, chimpanzees are so far from acquiring them, spontaneously or not. One must hypothesize some yet unknown qualitative gap between animal and human *general* learning abilities. Invoking such "pre-adaptation" remains, for now, non-parsimonious. Not only is the emergence of "pre-adaptations" not accounted for in iterated learning models and more broadly in non-functional models, but their subsequent assemblage into a functional whole remains mysterious as well. Bio-functional approaches to language emergence avoid the "pre-adaptation" trap. They do not attempt to explain why a given feature did *not* occur in other lineages by invoking the lack of required "pre-adaptations."

Language is not a marginal habit that would be incidentally used in our species. It has dramatic influence, not merely on survival, but on differential reproduction, which is what determines natural selection. Individuals who fail to be relevant are excluded from social networks and become preferential victims (Dessalles 1998b; 2007). Given the crucial impact of conversational performance on reproductive success, it would be highly unlikely that human brains could have evolved independently from language.

Language as shaped by social interaction

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Abstract: Language is shaped by its environment, which includes not only the brain, but also the public context in which speech acts are effected. To fully account for why language has the shape it has, we need to examine the constraints imposed by language use as a sequentially organized joint activity, and as the very conduit for linguistic diffusion and change.

I welcome Christiansen & Chater's (C&C's) contention that cognitive scientific approaches to language should take seriously the idea that language is adapted to its environment. Although C&C concentrate on the private cognitive and neural structures that each language user possesses, my commentary concerns a different aspect of the environment of language, one which is no less responsible for the shape language takes: namely, the public social-interactional setting in which language is learned and used, and which is the central conduit for the historical distribution and development of language in populations.

C&C consider the implications of a dual-inheritance model by which human genetic evolution proceeds in parallel with much faster processes of historical evolution of culture in domains such as kinship, social values, technology, and language (Cavalli-Sforza & Feldman 1981; Durham 1991; Richerson & Boyd 2005; cf. Enfield 2005; 2008, for language). A great discrepancy between the high speed of language change and the relatively low speed of genetic evolution drives C&C's argument that language (evolving historically) is adapted to the brain (evolving phylogenetically), rather than the other way around. This requires that language change be analyzed in evolutionary terms. To this end, C&C draw a parallel between the language system and the organism, as others before them have done. However, this may not be the most apt analogy. In genetic evolution, the organism serves as a vehicle for the replication of genes. In language, the vehicle for replication of linguistic units (e.g., words or constructions; Nettle 1999) is not the language system as a whole. The larger system is an aggregate of interrelated linguistic items. It may be stored in individual brains, or in linguistic descriptions, but it is not a vehicle for replication of linguistic units.

The vehicle by means of which linguistic items are used and diffused is the speech act (or utterance; Croft 2000). Through being used in speech acts, linguistic items maintain circulation in populations; and it is through this circulation that selection of linguistic variants takes place. Diffusion of linguistic variants involves not just brains, but a see-sawing process, from private mental states (conceptual representations, communicative intentions), to public states of affairs (speech acts), back to new brain states (interpretations of speech acts leading to new conceptual representations, new communicative intentions), and on to new states of affairs (more speech acts). It is a continual chain of transition from private to public to private to public, and so on (Sperber 2006) – as is the case in the historical evolution of cultural variants more generally (Richerson & Boyd 2005; Rogers 1995).

Linguists of many stripes recognize the privileged status of something closely akin to the speech act as the basic shape for linguistic organization: variously described, for example, as the "clause" (Foley & Van Valin 1984), "intonation unit" (Chafe 1994), "turn-constructional unit" (Sacks et al. 1974), "growth point" (McNeill 1992), and so on. Why should just this unit constitute the privileged shape for linguistic organization? The answer is that the speech act or utterance is a basic unit at the level of informational delivery; that is, an utterance conveys one idea at a time (Pawley & Syder 2000), thereby effecting one increment of social action at a time (Heritage & Atkinson 1984). Is there something about the brain that privileges linguistic units of just this shape? Or are there other reasons that the speech act (utterance, clause, turn, etc.) should be a privileged shape for linguistic structure?

There is reason to think that the one-speech-act-at-a-time structure of grammar is shaped by contingencies of the conversational settings in which language is learned, used, and diffused. Human social interactions are sequences of moves and counter-moves (Goffman 1964), each move being a response to an immediately prior move, and a stimulus for a subsequent move (Sacks et al. 1974). This pattern of rapid response and counter-response is what characterizes free conversation, the basic format for language acquisition and use in everyday life.[1] Once we view the use of language in human interaction as a type of joint activity (Clark 1996b), and not just an event of information processing that happens to involve more than one brain (Hutchins 1995; 2006), then we see how language is shaped by the sequential contingencies of social interaction. Grammar's basic "chunking" delivers minimal units, such that each unit contributes to a sequence of social interaction as an adequate response to a prior unit (Schegloff 2006). To be effective, any such unit increment must not only be successfully formulated by a speaker, but must also be successfully comprehended by a listener. The organization of language in chunks of "turn" size gives interlocutors the opportunity to monitor misfirings and misunderstandings as soon as they happen, and to correct them if necessary (Schegloff et al. 1977). This co-contingency of unit contribution and response may be argued to serve as a direct determinant shaping linguistic organization, including many of the properties of "Universal Grammar" that C&C are looking to explain without reference to an innate language faculty (cf. Tomasello 1995; 2004).

In sum, the acquisition and use of language involves not just the brain's private structures, but also the public patterns of co-dependent, interlocking contributions to sequences of social interaction. The preferred locus of grammatical organization – the speech act – is an optimal solution to multiple constraints of information-packaging in an environment where not just formulation of social action, but the possibility of timely monitoring of intersubjective understanding and appropriateness of response is as definitive of linguistic well-formedness as any arbitrary unit of sentence-level syntactic structure.

NOTE

1. Surprisingly little is known about the structure of language in conversation, apart from a rich body of work on English (see Schegloff [2007] and references therein). Comparative work on conversational structures is beginning to appear (see Enfield & Stivers 2007; Sidnell 2007).

The origin of language as a product of the evolution of double-scope blending

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Abstract: Meaning construction through language requires advanced mental operations also necessary for other higher-order, specifically human behaviors. Biological evolution slowly improved conceptual mapping capacities until human beings reached the level of double-scope blending, perhaps 50 to 80 thousand years ago, at which point language, along with other higher-order human behaviors, became possible. Languages are optimized to be driven by the principles and powers of double-scope blending.

Christiansen & Chater (C&C) are correct in their claim that it is implausible that language as we know it is the product of biological evolution for a complex, language-specific endowment. As they point out, this is not in itself an unusual claim. For example, Hauser et al. (2002) argue that the sole language-specific capacity might be recursion, and that even recursion might not be language-specific. However, our reasoning to this claim is quite different from C&C's. Language as we know it requires advanced capacities for meaning construction. Any view of language as having been active in quasi-advanced forms before about 50 thousand years ago, advancing further by refinements, runs up against the unlikelihood that human beings who enjoyed these near-modern capacities of meaning construction through language

(blending, hypothetical and counterfactual thought, negatives, framing, mappings of many sorts, viewpoint and perspective, metaphor, speech acts, deixis, etc.) failed to use them to achieve even the rudiments of the other human higher-order cognitive achievements that we know require those very same mental resources: art, music, mathematical and scientific discovery, religious practices, representation, fashion, advanced social cognition, and so on.

The archeological record (Klein 1999; Mithen 1996), genetic record (Cavalli-Sforza 2000; Thompson et al. 2000), and modern understanding of the uniformity of conceptual mappings in multiple, superficially diverse areas of human behavior all converge to indicate that biological evolution slowly produced not language but, rather, capacities not specific to language, evolving along a cline of increasing power. Once those capacities reached a certain sine qua non stage on the gradient, language and other human singularities became possible (Fauconnier & Turner 2002; 2008; Turner 1996).

One (and perhaps *the*) mental operation whose evolution was crucial for language is conceptual blending (Coulson 2006; Coulson & Oakley 2000; 2005; Fauconnier & Turner 1998; 2002; Turner 1996). Conceptual blending is a fundamental mental operation whose rudimentary forms are evident in the mammalian line of descent. The most advanced form, double-scope blending, consists of integrating two or more conceptual arrays as inputs whose frame structures typically conflict in radical ways on vital conceptual relations, such as cause-effect, modality, participant structure, role-value, and so on, into a novel conceptual array whose frame structure draws selectively from the frame structures of the inputs and dynamically develops emergent structure not found in either of the inputs.

There is now massive evidence that double-scope blending is indeed a necessary feature of all the human singularities mentioned above, including language. Conceptual blending itself has been evolving since at least deep in the mammalian line. Once the stage of double-scope blending was achieved, the full range of human higher-order singularities became possible. They arose in concert, reinforcingly, in cultural time. The archeological record suggests that the stage of double-scope blending was reached not millions of years ago and not even at the stage of anatomical speciation for human beings (about 150 thousand years ago), but rather, more recently, perhaps 50 to 80 thousand years ago (Mithen 1996).

Grammatical constructions are products of conceptual mapping. Specifically, they are double-scope blends (Fauconnier & Turner 1996; Liddell 2003; Mandelblit 1997). Accordingly, the existence of language requires the capacity for double-scope blending. Because double-scope blending is necessary for these patterns of meaning construction, because grammatical constructions in general are not possible absent the capacity for double-scope blending, and because double-scope blending is necessary for equipotentiality – the amazing ability of language to be used effectively in any situation, not just those that fit a finite list of frames (Fauconnier & Turner 2002) – language (like other human higher-order conceptual singularities) appears only once mapping capacities have evolved to reach the stage of double-scope blending. Intermediate stages of the mapping capacities are useful and adaptive, but not for language, which demands equipotentiality. This explains the absence of intermediate stages of language as an observable product.

There is no evidence known to science of simple languages now or at any time during our phylogenetic descent, because there are no simple or rudimentary languages. Once the stage of double-scope blending is achieved, fully complex language comes on like a flood, in cultural time rather than in biological time. In the early twentieth century, scientists at last gave up the argument that the cave paintings of France and Spain could not date from the Upper Paleolithic. They had assumed that art must have gone through stages of increasing complexity and accomplishment, that it must have been simple at its birth. We argue that a century later, scientists must give up the same argument and the same mistaken assumptions about language.

There is evidence of simpler stages, not of language or art, but of the mental operation underlying these behaviors – conceptual integration. The more rudimentary forms of conceptual integration remain available to all human beings, who moreover use those simpler forms constantly. Arguably, the evolution of mapping capacities in human beings was adaptive, and took place in standard fashion, but left no "fossils" of the singularities (such fossils being "simpler" languages, "simpler" religions, and "simpler" drawings and cave paintings).

There is a long tradition, inherited by generative grammar from structuralism, of studying languages as formal systems, divorced from their deeper purpose, which is to prompt for elaborate meaning construction (Dancygier & Sweetser 2005; Hougaard & Oakley 2008; Liddell 2003). In contrast to this tradition, recent research offers very strong evidence for uniform conceptual mapping capacities that cut across domains. The cultural construction of classical mathematics through successive double-scope conceptual blends is demonstrated in detail in Lakoff and Núñez (2000). Similar detailed research now exists for religion and magic (Slingerland 2008; Sørensen 2006); design (Imaz & Benyon 2007); technology (Hutchins 2005; Pereira 2007; Williams 2005); poetry, fiction, and theater (Dancygier 2006); music (Zbikowski 2001); social cognition (Turner 2001); and, of course, grammar (Fauconnier & Turner 1996; Mandelblit 1997). Strikingly, none of these highly typical human domains of action and meaning are possible without double-scope conceptual blending, and their emergence takes place at the beginning of our own cultural time, circa 50 thousand years ago (Klein 1999).

We concur with C&C's second principal claim: that language is shaped by the brain. But again, we reach this conclusion by a different route of reasoning. Once the brain, through evolutionary time, acquired the capacity for double-scope blending, language, along with other human singularities, became possible. Language is only one of the universal surface manifestations of the deeper unity of highly human-specific meaning construction, requiring double-scope capacity, and constrained by the constitutive and governing principles of integration (Fauconnier & Turner 2002). Languages can then change through cultural time subject to such constraints, and the well-studied pressures and mechanisms of diachronic linguistics. It remains highly doubtful that such change makes languages better adapted, as C&C wish to think. However even if it did, the capacity for more or less adapted, but fully expressive, languages, attested only in recent cultural time, would remain on their account an unexplained singularity. Accordingly, we view C&C's speculations about linguistic change in cultural time as orthogonal to the central problem of how evolving mental capacities reached a critical point where human singularities, including language, became possible.

Co-evolution of phylogeny and glossogeny: There is no "logical problem of language evolution"

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Abstract: Historical language change ("glossogeny"), like evolution itself, is a fact; and its implications for the biological evolution of the human capacity for language acquisition ("phylogeny") have been ably explored

by many contemporary theorists. However, Christiansen & Chater's (C&C's) revolutionary call for a replacement of phylogenetic models with glossogenetic cultural models is based on an inadequate understanding of either. The solution to their "logical problem of language evolution" lies before their eyes, but they mistakenly reject it due to a supposed "circularity trap." Gene/culture co-evolution poses a series of difficult theoretical and empirical problems that will be resolved by subtle thinking, adequate models, and careful cross-disciplinary research, not by oversimplified manifestos.

A core claim of the target article by Christiansen & Chater (C&C) – that languages change, and that theories of language evolution must take this into account – is undoubtedly correct. Language change, or "glossogeny" (Hurford 1990), plays an important role in language evolution, recognized and explored by many scholars (Deacon 1997; Fitch 2005; 2007; Keller 1994; Kirby 1999; Kirby et al. 2007; Lieberman et al. 2007; Pagel et al. 2007). C&C review some good reasons why. But their core assertion that "Language has been shaped by the brain, rather than vice versa" (sect. 4, para. 9) is based on a false dichotomy. The explanatory role of glossogeny is complementary to, not in competition with, that of biological evolution. The keyword is "co-evolution" (Deacon 1997; Dunbar 1993; Durham 1991; Feldman & Laland 1996). C&C's argument pervasively mixes metaphors, uses slippery terms like "language" and "Universal Grammar (UG)" chimerically and without definition, and fails as a contribution to this literature. The "logical" problem is not with the logic of evolutionary reasoning, but with C&C's understanding of it.

C&C's rejection of the possibility of biological evolution of a human-specific language capacity is grounded on a misguided rejection of what they mistake for "circular" reasoning. One of Darwin's core insights was that the biological past influences the evolutionary future. Despite the power of natural selection to tailor organisms to their environment, adaptation occurs within a limited range determined by past evolutionary history. Thus, inevitably, today's "effects" are tomorrow's "causes." Despite the essential correctness of this way of thinking, it has been dogged since its inception by accusations of circularity and tautology (Mayr 1982), which periodically reappear due to a failure to fully understand the nature of biological causality (e.g., Moorhead & Kaplan 1967; Peters 1976; Stebbins 1977). C&C's "logical problem of language evolution" (target article, Abstract) provides another example of this failure, addressing problems easily solved with standard evolutionary reasoning. But C&C rule out such solutions due to their supposedly "obvious" circularity. Like many previous critics of evolutionary theory, C&C have fallen into the "linearity trap": thinking that the only logically permissible form of causal reasoning is a one-way movement from causes to effects. Such reasoning is inadequate for understanding biological causality, in development or evolution, which is far more complex and indeterminate than this: multiple effects at one point in time become the causes of subsequent effects in a never-ending cycle (Mayr 1961; 1988). Cyclicity is a core characteristic of the phenomenon under study; and by ruling out appropriately cyclical forms of explanation under the heading of "circular reasoning," C&C create a problem where there is none.

C&C argue that languages change so fast that any biases to learning a particular language, selected in one generation, will be unsuited to a later version of that language generations later. If this "logical problem of language evolution" is indeed as severe as C&C claim, it is not just linguists who should be worried: any biologist interested in adaptation to a rapidly changing environment (e.g., individual learning) or culturally transmitted system (e.g., bird or whale song) should be alarmed. Birdsong is a well-studied example of "animal culture" (Catchpole & Slater 1995; Marler & Slabbekoorn 2004). Many birds learn their song, and due to accumulated errors, the songs of local populations diversify, form dialects, which gradually change over time (Baker & Cunningham 1985). Modern biologists universally accept the notion that birds have an "instinct to learn" not just song in general, but their species-specific song (Gould & Marler 1987; Marler 1991), an outcome that should be impossible if C&C were correct. Have all these birdsong biologists fallen into the "circularity trap"? Of course not. Understanding gene/culture co-evolution requires more sophisticated models, and more subtle reasoning, than the simplistic options considered by C&C (cf. Boyd & Richerson 1985; Marler 1991; Nottebohm 1972).

Consider what happens when some new culturally transmitted display arises for non-genetic reasons (e.g., a copying error) and proves popular among display recipients. For whatever reason, some members of the current population may find this cultural variant easier to master than do others; and if there is any genetic basis for this difference, this biological variant will increase in frequency in subsequent populations: the alleles responsible may experience consistent positive selection. Crucially, some types of constraints (e.g., a proclivity for specific details) will have no long-term advantage, because of rapid dialectal change. For other constraints (e.g., better sequence memory), the constraint may be abstract and general enough to apply across time, to many different chronodialects. Rapid cultural change thus selects for abstract constraints on learning, just as rapid change in the physical environment selects for "generalist" species that solve problems via plastic responses to the environment (e.g., biased learning) rather than fixed instincts (West-Eberhard 1989). The "instinct to learn" continues to evolve biases and constraints, but for abstract features rather than details. Similarly, language change does not entail a cessation of selection. Rather, consistent positive selection occurs only for variants capable of abstracting over rapid glossogenetic variation. A proto-constraint ("UG1") shapes proto-language, which influences further evolution of the constraint ("UG2"), which shapes later glossogeny, and so on. Far from it being "inevitable" that UG would adapt to "*specific* word order, phonotactic rules, inventory of phonemic distinctions, and so on," as C&C claim (sect. 3.2.3, para. 2, emphasis theirs), language change makes this outcome extremely unlikely. This conclusion does not involve "circular reasoning," just a clear recognition of the essentially cyclical nature of evolution itself.

In a recent chapter inquiring whether language evolution is the "hardest problem in science," Christiansen and Kirby correctly assert that language is the "most complex behaviour we know of" (Christiansen & Kirby 2003). If so, the real traps for evolutionary approaches to this problem are oversimplification and a reliance on inappropriate models, metaphors, and preconceptions. By oversimplifying the nature of genes, evolution, the brain, and language, C&C do a disservice to the hypothesis they intend to champion. Increases in our understanding of language demand sophisticated models of the co-evolutionary interplay between ontogeny, glossogeny, and phylogeny, not a simplistic replacement of one by the other.

Universal Grammar? Or prerequisites for natural language?

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Abstract: This commentary aims to highlight what exactly is controversial about the traditional Universal Grammar (UG) hypothesis and what is not. There is widespread agreement that we are not born "blank slates," that language universals exist, that grammar exists, and that adults have domain-specific representations of language. The point of contention is whether we should assume that there exist unlearned syntactic universals that are arbitrary and specific to Language.

The notion of Universal Grammar (UG) is generally understood to embody a particular hypothesis, namely, that some substantial portion of human language is based on universal domain-specific syntactic principles that are biologically determined ("innate" or unlearned). The UG Hypothesis thus involves four interrelated claims:

1. Domain-specificity: Language acquisition is constrained by representations or principles that are specific to language.
2. Universality: These representations or principles are universal.
3. Innateness: These representations or principles are not *learned.*
4. Autonomous syntax: These representations or principles require reference to syntax, not to possible functional correlates of syntax.

Versions of each of these claims, taken independently, are not at all controversial. As Christiansen & Chater (C&C) make clear, no one believes that language arises from nothing. Our biological endowment is what separates us from the Amazon horned frog and is what ultimately ensures that humans have language while frogs do not. This is not the issue; the question is whether what separates us includes unlearned linguistic (i.e., *domain-specific*) representations concerning syntax. Generalizations about universals of human conceptual structure or about the human vocal tract do not provide evidence of Universal *Grammar* insofar as Universal Grammar is understood to be about grammar.

It is likewise clear that learning itself requires prior biases of one sort or another, since without any a priori similarity metrics or attentional biases, a system would not know on what basis to generalize; all input would be weighted equally or in some random fashion. But again, this general fact in no way requires that the metrics or biases must be domain-specific. Clearly, too, everyone recognizes that there are some language universals; the question is whether the universals make reference to autonomous syntactic generalizations, or whether instead they are explicable in terms of domain-general abilities and/or the semantics or pragmatics of the constructions involved (cf. Bates 1993; Goldberg 2006; Newmeyer 2005, for relevant discussion). In addition, we can all agree that adults have representations that are specific to language (for example, their representations of individual constructions); the question is whether these representations can be learned.

"Universal Grammar" has alternately been interpreted, not as a hypothesis, but as a definitional label. It can be defined as the "initial state" of the child before exposure to language, or as the set of constraints that narrows the set of all logically possible languages to the set of all humanly possible languages. Neither of these interpretations of UG embodies a controversial claim. Surely infants (at least younger prenatal) can be said to be in *some* initial state before they are exposed to language. Certainly there are constraints on the range of possible human languages. On either of these interpretations, once again, UG may not be specificallyabout grammar at all. The initial state and the set of factors that constrain human language may be comprised entirely of domain-general abilities and mechanisms that conspire to give rise to the inclination and ability to create, learn, and use language.

Everyone also understands that language must be compatible with the human brain in that processing mechanisms and social forces are recognized to constrain language.[1] Chomsky himself has recently emphasized the role of domain-general processes. In fact, he has acknowledged that he remains unconvinced by any proposals for domain-specific innate syntactic representations or principles, with the (possible) exception of recursion, noting, "We hypothesize that FLN [the domain-specific Faculty of Language] only includes recursion" (Hauser et al. 2002, p. 1569).[2]

The target article by C&C highlights the challenges that defenders of the four interrelated claims (listed above) face in detailing how unlearned, communicatively arbitrary universals of grammar might have evolved (see also, Deacon 1997; Elman et al. 1996). Moreover, while it made sense for researchers to explore the UG Hypothesis at the time it was proposed (Chomsky 1965), we are now in a better position to appreciate the power of statistics, implicit memory, the nature of categorization, emergent behavior, and the impressively repetitive nature of certain aspects of the input.

In order to avoid prejudging whether any of the necessary abilities and constraints on language are domain-specific (specifically syntactic), a better term than Universal Grammar might be *Prerequisites for Natural Language*. As Liz Bates used to say, "It's not a question of Nature vs. Nurture; the question is about the Nature of Nature" (Bates 1993).

Of course, if universal syntactic representations have not evolved biologically, then various questions immediately come to the fore, many of which are briefly discussed by C&C. What domain-general processes account for each cross-linguistic regularity? Why are there impressive generalizations within any given language? What distinguishes us from other primates such that only we spontaneously create and learn language? How exactly is language learned and processed? More generally, what exactly are the Prerequisites for Natural Language and how do they interact to yield the constrained complexity that is language? These are exactly the questions that are currently the focus of a tremendous amount of ongoing work (cf. references in the target article).

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NOTES

1. It is possible to agree with C&C's and others' arguments that our brains have not likely evolved to encode a complex system of arbitrary constraints on grammar, without embracing the notion that languages evolve to suit the human brain. Surely it is wars, assimilation, and dispersion, not processing difficulty, that lead to language spread (or death, depending on which side of the spear a speaker is on). Also, Creole specialists may well balk at the idea that "language has adapted through gradual processes of cultural evolution [in order] to be easy to produce and understand" (target article, sect. 1, para. 3). This would seem to imply that newer languages might be less easy to learn or use than older, more highly "evolved" languages, but there is no evidence that this is the case. Each natural language must satisfy the simultaneous and potentially conflicting constraints of expressive power, learnability, and processing ease.

A more natural perspective that C&C adopt in other parts in their article is that combined pressures of learnability, processing ease, and expressive power operate at the level of individual constructions. Individual words and constructions do change (or "evolve") to meet the changing demands of the overall system, as well as demands of external cultural forces. This insight harkens back to the structuralists and has recently received renewed attention (e.g., de Saussure 1916/1959; Ellis 2002; Enfield 2002).

2. See Pinker and Jackendoff (2005) for arguments against recursion being domain-specific and for other candidate domain-specific attributes. Their suggestions emphasize speech and semantics more than universal principles of syntax.

Intersubjectivity evolved to fit the brain, but grammar co-evolved with the brain

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Abstract: We propose that some aspects of language – notably intersubjectivity – evolved to fit the brain, whereas other aspects – notably grammar – co-evolved with the brain. Cladistic analysis indicates that common basic structures of both action and grammar arose in phylogeny six million years ago and in ontogeny before age two, with a shared prefrontal neural substrate. In contrast, mirror neurons, found in both humans and monkeys, suggest that the neural basis for intersubjectivity evolved before language. Natural selection acts upon genes controlling the neural substrates of these phenotypic language functions.

While we concur with Christiansen & Chater's (C&C's) well-reasoned thesis that "language has been shaped to fit the human brain" (target article, Abstract), we see co-evolution of the brain and human language as an additional process. Here we critique a few assumptions implicit in C&C's argument and buttress our claim that, while language evolved to fit the human brain, the brain and language also co-evolved.

The richest source of evidence regarding the co-evolution of language and the brain is overlooked by C&C: cladistic analysis. The study of a clade – a group of species sharing a common ancestor – allows inferences about traits likely to have been present in a common phylogenetic ancestor. Here, the relevant clade consists of *Homo sapiens*, *Pan paniscus* (bonobos), and *Pan troglodytes* (chimpanzees). Cladistic analysis fits with C&C's conclusion that human "language does not involve any qualitatively different mechanisms compared to extant apes, but instead a number of quantitative evolutionary refinements of older primate systems"(sect. 6.5, para. 3). Similarities in functional brain structures across the clade, paired with similarities in behavioral phenomena that correspond to simple forms of human language, lead to probable inferences that both brain and behavior co-evolved after the phylogenetic split of the species about six million years ago, producing larger brains, with particular expansion in the prefrontal cortex, and complex human language.

Concerning the co-evolution of brain and language, we disagree with the assumption that an adaptationist position towards the evolution of language entails viewing "arbitrary principles of UG" (sect. 2, para. 6) as genetically encoded. By offering an alternative to arbitrary UG (Universal Grammar), we obviate the need to solve C&C's *"logical problem of language evolution"* (target article, Abstract, their emphasis). Rather, we point to the structure of action as the genetically encoded basis of language structure and meaning (Greenfield 1978; 1991; Greenfield & Lyn 2006). Examining action structure as the phylogenetic origin of grammar provides new and different evidence for the authors' notion that "language may be rather less arbitrary than at first supposed" (sect. 8, para. 1).

Both apes and human children structure their semiotic combinations to express actions composed of semantic elements such as action, agent, object, and location (Greenfield & Lyn 2006). The expression of these basic action structures, such as action-agent or agent-object, by young members of the human, bonobo, and chimpanzee species became, on our theory, the building blocks for more complexity in both the phylogeny and ontogeny of human language (Greenfield 1978; Greenfield & Lyn 2006; Greenfield & Smith 1976; Greenfield et al. 1972). Particularly important to the connection between action and grammar are manual actions, including gesture. Indeed, an intermediate ontogenetic stage between single symbols and symbolic combinations typical of proto-language consists of a gesture combined with a symbol throughout the clade (Greenfield et al. 2008).

This integration of hand and mouth is basic to the ontogeny and phylogeny of proto-grammar, which may not be as variable as the authors assert. C&C use cultural variability of proto-language to dismiss co-evolution of brain and language. However, commonalities in the ontogeny of language across members of the clade (and across various human languages) suggest that proto-language is more constant than C&C hypothesize. These universal and cross-species features include cross-modal integration of indexicality and representation (e.g., gesture plus word in the communication of young hearing humans), plus structures expressing relations such as agent-action and action-object (Greenfield & Lyn 2006; Greenfield et al. 2008).

On the neural level, a key neural substrate for linguistic grammar – Broca's area – controls the processing of grammar of action tasks in human adults (Molnar-Szakacs et al. 2006). Mirror neuron research supports this connection between grammatical structure and action structure. Mirror neurons for motor actions are found in Broca's area (Iacoboni et al. 1999) and in Broca's homologue in monkeys (Rizzolatti & Arbib 1998). Here is neural evidence that grammatical structure may be an evolutionary exaptation of the structure of action. Lateralization of the ape homologue of Broca's area and asymmetry in its activation during gestural communication further suggest a similar substrate across the clade (Cantalupo & Hopkins 2001).

A comparison of the microscopic anatomy of the *planum temporale* (Wernicke's area in humans) between nonhuman apes and humans shows that only humans have asymmetrically wider and denser mini-columns in the left *planum temporale* (Buxhoeveden et al. 2001). This micro-structural lateralization specific to human primates suggests that increases of connectivity between perisylvian regions (such as Broca's and Wernicke's areas) may have coincided with the evolution of language (Catani et al. 2005). Similarities and differences in ontogeny, behavior, and anatomy across the clade suggest that C&C's brilliantly argued assertion that language evolved to fit the brain should be tempered by recognizing the importance of the co-evolution of language and the brain.

Intersubjectivity may be an important area in which language evolved to fit the brain. Like C&C, we reject Chomsky's claim that the communicative function of language was secondary to its representational function evolutionarily. A mirror neuron system adapted for relating self-generated actions to others' behaviors may have provided the intersubjectivity necessary for the evolution of language. The existence of a mirror neuron system in monkeys and humans (Rizolatti & Arbib 1998) implies a very old pre-linguistic origin of intersubjectivity and therefore fits with C&C's thesis that language evolved to fit the human brain.

Intersubjectivity allows people to learn language by co-construction whereby the conversational partner's contribution becomes part of one's own communication (Greenfield & Smith 1976; Scollon 1979). Mirror neurons enable imitation in humans (Iacoboni et al. 1999), a very basic form of dialogue. Repetition (imitation with varying pragmatic forces) is an essential part of both co-construction and the ontogeny of pragmatics shared across humans and apes (enculturated into interspecies communication) (Greenfield & Savage-Rumbaugh 1993; Keenan-Ochs 1977; Tannen 1987).

C&C note four constraints upon the evolution of human language: thought, perceptuo-motor factors, cognition, and pragmatics. To these the preceding argument implies that we must add a fifth: ontogeny. The way in which language develops constrains mature language: an examination of ontogenies across the clade necessitates the inclusion of this constraint. In final conclusion, we assert that (1) both co-evolution and brain-first evolution are processes in the evolution of language, and (2) both intersubjectivity and the structure of action provide phenotypic expressions of the genetic bases for the evolution of human language.

Why and how the problem of the evolution of Universal Grammar (UG) is hard[1]

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Abstract: Christiansen & Chater (C&C) suggest that language is an organism, like us, and that our brains were not selected for Universal Grammar (UG) capacity; rather, languages were selected for learnability with minimal trial-and-error experience by our brains. This explanation is circular: Where did our brain's selective capacity to learn all and only UG-compliant languages come from?

The problem of the evolutionary origins of Universal Grammar (UG) is not as readily solvable as Christiansen & Chater (C&C) suggest.

UG is a complicated set of grammatical rules, but not the ones we learned in school. We were never taught them, we are not aware them, we cannot put them into words, and we would not recognize them if they were explicitly told to us by a professional grammarian. Yet we all "know" the rules of UG "implicitly," because they are the rules that make us able to produce all and only the sentences that are grammatically well formed, according to UG. It is rather as if we all knew implicitly how to play chess – we could make all and only the legal moves – yet we had no explicit idea what rules we were following.

The rules of chess, however, are simple; we learned them, and we can verbalize them. UG's rules are abstract, complex, and technical. Since Chomsky first discovered the existence of these rules, linguists have gradually been figuring them out through decades of hypothesis, trial, and error, guided by the grammatical intuitions we all share about what can and cannot be said. The result is a set of rules that allow all and only the sentences we all recognize as well formed, and disallow all those we recognize as ill formed. That set of rules turned out to have some surprising properties. UG turned out to be universal: All languages obey the very same set of rules. But the most surprising property was that children do not learn the rules of UG itself.

Children cannot learn the rules of UG because they are too complicated to learn by observation and trial and error on the basis of the information available to the language-learning child. Nor are they taught by explicit instruction: Before Chomsky, no one even knew the rules, let alone taught them, even though our species had been speaking language for a hundred thousand years.

The reason the child cannot learn UG is that the *data* from which the rules of UG would have to be learned do not contain anywhere near enough of the information needed to infer the rules from them. This is called the "poverty of the stimulus." In order to be learned at all, the rules of UG would have to be learnable through trial and error, with error-correction, just as chess rules have to be, when we learn them without explicit instruction: I try to move my bishop in a certain way, and you tell me, "No, that's not a legal move, this is," and so on. Children cannot learn the rules of UG that way because they basically never make (or hear) any UG errors ("wrong moves"). Hence, children never get or hear any UG error-corrections.

It is not that children speak flawlessly from birth. But the little the child experiences during the relatively brief period of transition from being unable to speak to being able to speak *does not involve any errors (or error-corrections) in the rules of UG*, either from the child or from the speakers the child hears. There are conventional grammatical errors and corrections aplenty, but no UG violations produced, heard, or corrected. UG rules are never broken, never corrected, hence never "learned." Therefore, they must already have been inborn.

But that raises the hard question of the evolutionary origin of those inborn rules. Evolution has more time available than the child, but it has an even more impoverished database: What would serve as error-correction, and what would count as right and wrong, in order to shape UG in the usual Darwinian way, through trial-and-error genetic variation and selective retention, based on advantages in survival and reproduction?

In explaining the origins of other complex biological structures, such as fins, wings, and eyes, or biological functions, such as the capacity to see, learn, or reason, there is no problem in principle for the usual kind of evolutionary trial-and-error explanation. But with UG there is a deep problem in principle (Harnad 1976). The problem is not just UG's complexity but that *UG has no apparent adaptive advantages*. For although a professional grammarian's lifetime is long enough to work out most of UG's rules explicitly by trial-and-error induction, it turns out that (with the possible exception of a few small portions of UG governed by optimality constraints) *no logical or practical advantage has yet been discerned that favors what UG allows over what it disallows, or over an altogether different set of grammatical rules* (perhaps even a much simpler and learnable set).

C&C rightly express skepticism about alternative "piggy-back" theories of the evolutionary origin of UG. There is no credible "precursor" with a prior adaptive advantage of its own that could later have been "co-opted" to do the duties of UG as well. But C&C's alternative proposal is no more convincing: C&C say that language, too, is an "organism" (target article, Abstract), like people and animals; that it too varies across generations, historically; and that the shape that language took was selectively determined by the shape the brain already had, in that *only the languages that were learnable by our brains successfully "survived and reproduced."*

The trouble with this hypothesis is that it is circular: We were looking for the evolutionary origin of the complex and abstract rules of UG. C&C say (based on their computer simulations of far simpler rule systems, not bound by the poverty of the stimulus): Do not ask how the UG rules evolved in the brain. The rules are in language, which is another "organism," not in the brain. The brain simply helped shape the language, in that the variant languages that were not learnable by the brain simply did not "survive."

This hypothesis begs the question of why and how the brain acquired an evolved capacity to learn all and only UG-compliant languages in the first place, despite the poverty of the stimulus – which was the hard problem we started out with in the first place! It would be like saying that the reason we are born already knowing the rules of chess without ever having to learn them by trial and error is that, in our evolutionary past, there was variation in the games (likewise in "organisms") that we organisms tried to play, and only those games that we could play without having to learn them by trial and error survived! (That still would not even begin to explain what it is about our brains that makes them able to play chess without trial and error!)

This circularity is partly a result of a vagueness about what exactly is the target of language evolution theory. Pinker and Bloom (1990) had already begun the misleading practice of freely conflating evolutionarily unproblematic questions (such as the origins of phonology, learnable aspects of grammar, vocabulary, "parity") with the one hard problem of the origins of UG, which *specifically concerns the evolutionary origins of complex rules that are unlearnable because of the poverty of the stimulus*. Language, after all, is not just grammar, let alone just UG. If, on the one hand, the adaptive value of language itself (Cangelosi & Harnad 2001; Harnad 2005; 2007) could have been achieved with a much simpler grammar than UG (perhaps even a learnable one), then the evolutionary origin and adaptive function of UG becomes all the harder to explain, with C&C's historical variation in the language "organism'" occurring far too late in the day to be of any help. If, on the other hand, the adaptive advantages of language were impossible without UG, then we are still left with the hard problem of explaining how and why not.

Chomsky (2005a) himself has suggested that UG may be a *necessary* property of being able to think at all. He has been right about so much else that this possibility definitely needs to be taken seriously. But to solve the hard problem, we would also have to explain *how* UG is logically or functionally necessary in order to be able to think at all.

NOTE

1. An unabridged draft of this commentary is available online at: http://cogprints.org/6008/.

Niche-construction, co-evolution, and domain-specificity

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Abstract: That language is shaped to fit the human brain is close to the Chomskyan position. The target article by Christiansen & Chater (C&C) assumes an entity, "(the) language," outside individual heads. What is the nature of this entity? Linguistic niche-construction and co-evolution of language and genes are possible, with some of what evolved being language-specific. Recent generative theory postulates much less than the old Universal Grammar (UG).

I have much sympathy with the general view advocated by Christiansen & Chater (C&C) in the target article. But I find some disturbing problems with its particular emphases.

In classic generative grammar, the *explanandum* is the distinctive features of human language, and the *explanans* is the postulated LAD (language acquisition device) or UG (Universal Grammar). Further, UG is said to reside in the human brain. Thus, classic generative grammar explains why language is the way it is because of innate properties of the human brain. How does this view differ from the position taken in the target article, that "language has been shaped to fit the human brain" (Abstract)? In both cases, the brain has certain properties first, and then language grows to fit those properties. There are differences between the two positions, but these differences are rather subtle.

The first difference to notice is the perfect tense in "has been shaped," which invokes a diachronic, evolutionary process. The classic generative position accords no explanatory power to evolution, or to any diachronic processes (outside of ontogeny). In the classic view, languages grow their characteristic form, in toto once in each human lifetime, with every person's ontogeny, just as an organ grows. The slow, cumulative historical process advocated by C&C is surely plausible. But then the comparison with a bodily organ can no longer hold, because successive generations do not share the same physical organs. So the thing that grows, a language, has to be something outside of individuals. This risks getting Platonic, and C&C do not address this danger. It can be averted by stating that there is enough faithful, mind-external record of the whole structure of a language in the total ambient experience of each child. And this total ambient experience is provided by a society of other individuals who are all themselves at various stages of acquiring their own internalized representations of the language, in response to their own experiences of it. The "it" here is the language, a slowly moving target, as the authors point out. The classic I-Language/E-Language distinction is not undermined here. But the E-Language is given a status as an evolving social entity, which has a real causal influence, worth studying and not impossible to study, on the successive I-Languages of its speakers.

C&C argue against the view that human genes have adapted to a specifically "linguistic" environment. Throughout section 3.2 of the target article, there is a subtle vagueness about what is meant by "linguistic" and "language," the entity to which UG may have adapted. It would be absurd to suggest that during the course of recent human biological evolution, fully-fledged languages like French, Arabic, and Tamil existed, and that such languages with their rich structure constituted the environmental challenge to which the human genome adapted. To attack this view is to attack a straw man, as no one advocates recent adaptation to the detailed structure of fully modern languages.

But the remote ancestors of human languages were only in the barest ways like modern human languages. (This excludes the remote possibility that modern human languages suddenly appeared, fully formed, as a result of some macro-mutation or saltation.) Just around the dawn of our species, there would have been rudimentary genetic dispositions, different from those in our ape ancestors, biasing us toward acquiring communication systems of some rudimentary sort, the remote forerunners of modern languages. Now these rudimentary forms were not yet "linguistic" in the modern sense, but they differed from anything previously existing. The target article only considers in a last brief section (sect. 8.2) the possibility of a kind of niche-construction in the specific domain of the unique type of communication embarked upon by proto-humans. Here C&C concede that there could have been natural selection for functional aspects of language. (Well, of course, whoever heard of natural selection for anything non-functional?)

Given that human language is spectacularly unique, and spectacularly functional, it would not be surprising to find some overlap between the unique aspects and the functional aspects. And this would give us domain-specificity of functional aspects of language. In this case, general cognitive capacities, used in non-linguistic domains, such as navigation, planning, and recall of past events (all without the aid of inner speech), cannot be summoned up to explain the relevant features of language. I will be little more specific than C&C about what these unique-to-language features might be. But a few reasonable candidates are: (1) the ability to acquire a massive inventory of form-to-meaning mappings (vocabulary); (2) the ability to manage a communication system with duality of patterning (double articulation), that is, a system with two combinatorial layers, phonology and syntax; and (3) the ability to manage nested long-distance dependencies, where the co-dependent items are in no way represented outside the head of the producer while speaking. All human languages have these properties which must be mastered in a few years by the child; and, barring pathology, children achieve mastery spectacularly well. These properties are arguably specific to language only, and there could well have been runaway biological adaptation, with a feedback loop, to the embryonic beginnings of systems with such properties. One force driving such adaptation would have been the peculiar hominid social setup, with large groups of mutually cooperative individuals. This all needs to be argued in detail, but the idea is as well developed as any alternative suggested by C&C in the target article.

Finally, ironically, the target article mentions the difficulty of adapting to a moving target. The innate UG that the authors attack is itself a notoriously moving target. Their target is "the extremely rich and abstract set of possibilities countenanced by the principles of UG" (sect. 3.2.3, para. 1). The generative enterprise based on this formulation has been turned upside-down by the more recent insistence on minimalism and the proposal that all that is distinctive about human language is recursion. So maybe C&C are pushing at an open door, or flogging a dead horse. The issues raised by the authors are important, and always have been. These issues need further work – and in a positive empirical direction, please.

Language enabled by Baldwinian evolution of memory capacity

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Abstract: The claim that language is shaped by the brain is weakened by lack of clear specification of what necessary and sufficient properties the brain actually imposes. To account for human intellectual

superiority, it is proposed that language did require special brain evolution (Deacon 1997), but that what evolved was a merely quantitative change – in representation space – rather than a radically new invention.

To say that language is shaped by characteristics of the brain implies that to understand language evolution, we need to know how the brain's capabilities and limits apply to language. However, Christiansen & Chater (C&C) say little more than that the brain had developed the needed perceptual, motor, and general cognitive abilities before language emerged. In their own research and theorizing, C&C have steadfastly objected to the arguments of Chomsky, Pinker, and other researchers that seem to suggest that calling something we cannot explain "innate" excuses us from trying to understand how it works (grammar is an instinct – duh!). Yet C&C seem to have done something close to that here, saying that language evolution is shaped by the brain without telling us how. This could be a strategic divide-and-conquer step, but its use by the authors without explanation is disappointing. I take a stab here at rectifying the omission in a way that leaves the main idea intact: hypothesizing an important quantitative brain evolution that would have been a necessary enabler of cultural language evolution.

There has been dramatic progress in the last few decades, some of it attributable to Christiansen and Chater in various works, in creating and evaluating computational mechanisms that do much of what human brains do in acquiring and using language based solely on the kinds of language experience that all humans have. These models offer empirical examples of fundamentally simple mechanisms that learn to do things that have often been declared impossible to learn. I focus here on Latent Semantic Analysis (LSA; Landauer & Dumais 1997), and mention two others, the Topics model of Steyvers and Griffiths (2007) and the BEAGLE model of Jones and Mewhort (2007), which employ different means to achieve similar results in mimicking human use of many tens of thousands of words to convey meaning. Then I add some extrapolative conjectures on how these successes suggest ways in which culturally steered (Baldwinian) genetic evolution could have played a crucial role in language evolution by expanding something already important.

These models all learn to simulate human language phenomena solely by mathematical analysis of large-text corpora that closely resemble what average literate people have read. They all eschew any direct aid from language experts – such as grammatical annotations or semantic hierarchies – that must themselves be results of the causal mechanisms sought. Each in its own way achieves a representation of words and passages as numerical vectors that obey the compositional constraint that every meaningful passage be a combination of components chosen from the same set; for example, sets of English words or Chinese characters. All three models closely simulate human performance in language tasks, such as answering synonym tests and mimicking free association. For more examples, LSA learns word meanings at the same daily rate as children; and has come close to equaling humans in judging coherence of book chapters, the topical similarity of conversational utterances, the semantic similarity of test essays, and in identifying translated documents in widely differing languages when given only partially overlapping experience with them. (For more on these examples and many others, see Landauer et al. 2007.) Lest a reader be tempted to discount these achievements because LSA almost completely ignores grammar (reflecting an apparent assumption of grammar's near equivalence with language in the target article and elsewhere in the innateness debate), consider the following two observations: (a) in a study in which two independent expert readers and LSA each estimated the quality of substantive content of essays, the mutual information between LSA and humans was 90% of that between two humans; and (b) the possible information in a typical sentence attributable to word choice is about nine times that of word order (Landauer 2002).

Now for the conjecture on how Baldwinian evolution may have been essential to language. The fundamentally simple mathematics by which LSA learns and uses its word and passage vector representations requires a representational space of about 10^{13} bits.[1] (The other models make similar demands.) This is some 10,000 times the amount of learned information accumulated in a normal human lifetime (Landauer 1975). Of this, more than one-tenth is knowledge of word meanings. By this analogy, the space needed to support language is tauntingly similar to the increases in primate and human cortex size over the probable period of development of gesture, proto-, and fully *Homo sapiens sapiens* languages (Deacon 1997). Acknowledging some unresolved questions in this arena, it appears that language may have simply needed much more relevant brain space. Importantly, the new space was most likely the same kind of space – analogous to increasing general-purpose memory capacities in a computer – not something wonderfully novel like Universal Grammar (UG).

So, suppose that the explosive human cortical growth started with a mutational decrease in the usual amount of death of neonatal neural cells, and this let some early male get a tiny bit better at composing multi-utterance mating calls, which let him sire more people like him ... The resulting genetically adapted brain size growth would be no more mysterious, or take longer to happen, than the differentiation of Great Danes and Chihuahuas; and it could have eventuated in great vocabularies that made possible great minds that supported intelligent cultures that in time invented many grammars whose possibly equally simple underlying mechanisms we have not yet discovered. Learning how every one of more than 100,000 words relates to any other word, and how their combinations yield meaning, appears as complex and difficult to me as learning a grammar, yet succumbs to mathematical simulations, given enough space.

NOTE

1. "Representational space" is not the same as permanent memory storage space: the former includes locations where unique, transiently computed values need to be represented without interference.

Cortical-striatal-cortical neural circuits, reiteration, and the "narrow faculty of language"

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Abstract: Neural circuits linking local operations in the cortex and the basal ganglia confer reiterative capacities, expressed in seemingly unrelated human traits such as speech, syntax, adaptive actions to changing circumstances, dancing, and music. Reiteration allows the formation of a potentially unbounded number of sentences from a finite set of syntactic processes, obviating the need for the hypothetical "Narrow Faculty of Language."

What is missing from the otherwise excellent discussion presented by Christiansen & Chater (C&C) are insights from current studies on how brains might actually work. The traditional Broca-Wernicke theory, though straightforward, is wrong.

Neural circuits. Complex brains contain distinct neuroanatomical structures that perform local operations, such as processing tactile, visual, or auditory stimuli. However, an isolated neural structure or cortical area generally is not the "seat" of a complex behavior. Instead, a particular neural structure may support many anatomically segregated groups – *populations* – of neurons that carry out a similar "local" operation. Each neuronal population is linked to – *projects* to – an anatomically

distinct neuronal population in another region of the brain, forming a *neural circuit*. The circuit regulates an observable aspect of behavior, such as walking, talking, dancing, comprehending syntax, and so on. Moreover, within a given neural structure, distinct *anatomically segregated* neuronal populations may occur, that project to different brain structures forming multiple circuits that regulate other behaviors. Therefore, a given neural structure may be involved in different aspects of behavior, each regulated by a different circuit.

A class of *cortico-striatal-cortico* circuits involves links between cortical areas and the subcortical basal ganglia. Cummings (1993), in his review article, identifies five parallel basal ganglia circuits that are involved in motor control, cognition, attention, and other aspects of behavior. Disruptions in behavior seemingly unrelated, such as obsessive-compulsive disorder (Greenberg et al. 2000), schizophrenia (Graybiel 1997), and Parkinson's disease (Jellinger 1990), derive from the impairment of these neural circuits. Behavioral changes usually attributed to frontal lobe cortical dysfunction can be observed in patients having damage to basal ganglia (e.g., Flowers & Robertson 1985; Lange et al. 1992).

Reiteration. The basal ganglia enable humans to generate a potentially unbounded number of motor acts, such as words or dances, by the process of reiteration, selecting and sequencing a finite set of "pattern generators" that each specify a sub-movement. Individual motor pattern generators may entail selectional constraints, yielding hierarchical structures. Walking, for example, involves executing a heel strike at an appropriate point in a sequence of leg and foot sub-movements. The basal ganglia also reiterate *cognitive pattern generators* that constitute sub-elements of thought processes. Parkinson's disease (PD), which damages the basal ganglia, mostly sparing cortex, thus yields deficits such as tremors, rigidity, and disruptions in speech production. PD patients can have difficulty producing and comprehending sentences that have complex syntax (Grossman et al. 1991; 1993; Illes et al. 1988, Lieberman et al. 1990; 1992; Natsopoulos et al. 1993). As PD progresses, patients are unable to readily form or change cognitive sets (Cools et al. 2001; Flowers & Robertson 1985).

Neuroimaging studies confirm the essential cognitive role of the basal ganglia. Monchi et al. (2001) used functional magnetic resonance imaging (fMRI) to monitor brain activity of neurologically intact subjects in a version of the Wisconsin Card Sorting Test (WCST), which evaluates a person's ability to form and shift cognitive criteria. Bilateral activation was observed in the prefrontal cortex, basal ganglia, and thalamus. Dorsolateral prefrontal cortical areas were active when the subjects had to relate the current match with earlier events stored in working memory. Mid-ventrolateral prefrontal cortex, caudate nucleus, putamen, and thalamus were active when subjects had to shift to a different matching criterion. Stowe et al. (2004) used positron emission tomography (PET) imaging of neurologically intact subjects in a sentence comprehension study. The basal ganglia to dorsolateral prefrontal cortex circuit was active when subjects had to change their interpretation of an ambiguous sentence, confirming that basal ganglia set shifting manifests itself in language. Other neuroimaging studies show basal ganglia linked to cortex during sentence comprehension and word retrieval tasks (Klein et al. 1994; Kotz et al. 2003; Rissman et al. 2003; Stowe et al. 2004). In short, the basal ganglia act in concert with cortical areas of the brain to *reiterate* pattern generators in motor, cognitive, and linguistic tasks.

The "narrow faculty of language." The evidence noted here (cf. Lieberman 2000; 2002; 2006) suggests that the productive aspects of speech and syntax derive from cortico-striatal-cortico circuits that confer reiteration. This negates the most recent version of Universal Grammar (UG), the "narrow faculty of language" (NFL) (Hauser et al. 2002). The human and language-specific NFL supposedly is the key to *recursion*, which involves inserting identical elements, usually sentences (Ss), into a underlying phrase marker. Generative grammars since Chomsky (1957) claim the relative clause in a sentence such as, *The boy who was talking fell down*, derives from a sentence node "*S*" inserted into a hypothetical *underlying* sentence. In the 1957 system, transformational rules acted on the underlying sentence to yield the sentence that might be uttered or written. In Chomsky's (1995) current "minimalist" grammar, the syntactic rule *merge* inserts *S* nodes; the rule *move* and subsequent operations then rewrite the string of words to yield the sentence that one actually hears or reads. But is there any neurophysiological evidence for inserted *S* nodes in a hypothetical abstract structure formed by serial algorithms that have no demonstrable neural bases?

In contrast, "hard" data from imaging and behavioral studies of the linguistic deficits of PD, hypoxia (which has a profound effect on the basal ganglia; Lieberman et al. 1992; 2005), and the FOXP2 transcriptional gene studies (e.g., Lai et al. 2003; Vargha-Khadem et al. 1998) show that neural circuits involving the basal ganglia provide the productive capacity of syntax, as well as speech, and seemingly unrelated distinctly human traits such as music and dance.

The mark of evolution. Should we be surprised to discover that the basal ganglia, subcortical structures that can be traced back to anurans similar to present-day frogs, play a critical role in language? As Darwin (1859/1964) first observed, organs initially adapted to control one function take on "new" tasks. Seen in this light, the local motor sequencing operations in the subcortical basal ganglia appear to be precursors for similar operations in cognitive domains. In the course of evolution, they have been adapted to serve as a reiterative engine in cognitive domains including language.

Has anyone ever seen a chimpanzee dancing?

Perceptual-motor constraints on sound-to-meaning correspondence in language

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Abstract: The proposal that language has evolved to conform to general cognitive and learning constraints inherent in the human brain calls for specification of these mechanisms. We propose that just as cognition appears to be grounded in cross-modal perceptual-motor capabilities, so too must language. Evidence for perceptual-motor grounding comes from non-arbitrary sound-to-meaning correspondences and their role in word learning.

Christiansen & Chater's (C&C's) proposed account of the manner in which language and its acquisition are constrained by general cognitive mechanisms offers a compelling alternative explanation of language evolution and the relationship between language and the brain. We enthusiastically endorse C&C's proposal that language adapted to fit the general nature of human cognitive and neural processing. However, specification of the mechanisms by which cognitive and learning processes constrain language structure is critical. A particularly promising mechanism is perceptual grounding. Growing evidence suggests that both cognitive and language processing are grounded in multimodal perceptual-motor representations (Barsalou 1999; Clark 1997; Glenberg & Robertson 2000). We propose that this evidence informs the nature of cognitive processing and its relationship to the structure of language. C&C focus primarily on the

morphosyntactic structure of language. Our work extends these arguments to a consideration of lexical processing and the semantic system. In particular, we investigate the structural relationships between sound and meaning at the word or segmental level of analysis. We find that the basic structure of verbal symbols reflect a perceptual-motor grounding of language.

Sound-to-meaning mapping. Arbitrariness has long been considered a hallmark of spoken (and signed) language (de Saussure 1916/1959; Hockett 1977). Within the domain of semantics, the sound sequences that comprise individual words (unlike gestures or pictorial representations, for example) bear no resemblance to their referent, nor do they contain sounds consistently associated with specific meanings. There is no systematic relationship, the account goes, between particular phonemes or phoneme sequences and particular semantic features. Boutique phenomena, such as onomatopoeia, and language-specific phenomena, such as Japanese mimetics (Hamano 1998), have been regarded as notable and forgivable exceptions.

Arbitrariness offers a variety of cognitive advantages that have been highlighted in domain-general accounts of language. The flexibility, abstractness, generativity, referential specificity, and even memory advantages afforded by the arbitrariness of language are significant cognitive constraints that likely facilitate language learning and communicative effectiveness (de Saussure 1916/1959; Gasser 2004; Monaghan & Christiansen 2006). As languages evolve, pressures imposed by the constraints of the cognitive system facilitate gradual convergence on an arbitrary communicative system.

Recent evidence of reliable sound-symbolic aspects of meaning calls into question this notion of a completely arbitrary system of sound-meaning associations (Nuckolls 1999). For example, Berlin (1994) noted a reliable relationship between vowel height and size of animal within the domains of birds and fish in the Huambisa language. In a comprehensive inventory of phoneme-meaning correspondences in Indonesian, McCune (1983) suggested that virtually all words in this language include some sound-meaning correspondences (see also Hutchins [1998] and Bergen [2004] regarding sound-meaning correspondences in English). Classic work by Köhler (1947) and, more recently, by Ramachandran and Hubbard (2001), Maurer et al. (2006), and Westbury (2005) suggest that English-speaking adults and children will interpret non-words such as *maluma* and *bouba* as referring to round, amoeboid shapes and words like *takete* and *kiki* as referring to angular figures. Each of these findings suggests a cognitive association between particular sound sequences and meaning that guide and constrain the evolution of linguistic reference within a particular language.

Sound-to-meaning correspondence and learning. Our work explores (a) whether these sound-meaning correspondences extend cross-linguistically, and (b) the extent to which concordances between sounds and meaning facilitate word learning. This work was inspired in part by a study by Kunihira (1971) in which monolingual English speakers were asked to select which of two antonyms (e.g., fast vs. slow) was being expressed by spoken Japanese words. Kunihira found that subjects accurately inferred the correct meaning at above chance rates from the sound structure of these words alone. Our work has extended this basic finding to other languages, including Danish and Russian (Nygaard et al., in preparation).

We demonstrated the functional advantages of these non-arbitrary sound-to-meaning mappings, using a learning task in which monolingual English speakers were taught Japanese words that either had correct word-to-meaning mappings (e.g., *ue* meaning up), were mapped to the word's antonym (e.g., *ue* meaning down), or were randomly paired with a meaning (e.g., *ue* meaning slow). We found a consistent learning advantage for correct over incorrect mappings (Nygaard et al. 2008). This finding is consistent with C&C's assumption that properties of language, in this case residual non-arbitrary mappings, evolved because they ease learning and maximize cognitive efficiency.

Recent research from our lab and others also highlights how another type of sound-to-meaning mapping, namely prosody, constrains word meaning. Shintel et al. (2006) found not only that speakers modulated their speaking style (e.g., fundamental frequency or speaking rate) to reflect properties of a scene they were describing, but also that listeners were sensitive to these modulations and could reliably identify which of two possible scenes were being described based on speaking style. We have recently shown that both adults and children can reliably utilize prosodic information to infer the meaning of a novel word (see also Kunihira 1971), and that speakers reliably recruit distinct sets of acoustic properties to convey information about different semantic domains (Nygaard et al., in press; Sasso et al. 2005).

Multiple constraints on the structure of language. We have proposed that sound-meaning correspondences that facilitate learning stem from cross-modal perceptual-motor mappings. Such mappings would enable a speaker or listener to recruit acoustic-phonetic information as a guide to potential word meanings by evoking sensory-motor experiences that transcend the auditory modality. Consistent with C&C, we suggest that compelling cognitive pressures to generate arbitrary sound-meaning correspondences interact with a system that draws on cross-modal sound-meaning correspondences that offer more direct recovery of meaning. We propose that the advantages offered by perceptually grounded representations of spoken language compete with pressures to converge on an abstract, arbitrary system of meaning. Competing constraints placed on the system by the arbitrary versus non-arbitrary aspects of word meaning work in tandem to maintain a system that is optimally efficient given the structure and function of the human brain (Monaghan & Christiansen 2006; Monaghan et al. 2007). These competing constraints are consistent with C&C's assertion that "language will be the outcome of competing selectional forces" (sect. 7, para. 2). We conclude that if, as C&C argue, language has adapted to the brain, and if, as we argue, neural and cognitive constraints reflect a grounding in perceptual-motor systems, then these properties must necessarily permeate the fundamental nature and structure of language.

The potential for genetic adaptations to language

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Abstract: We suggest there is somewhat more potential than Christiansen & Chater (C&C) allow for genetic adaptations specific to language. Our uniquely cooperative social system requires sophisticated language skills. Learning and performance of some culturally transmitted elements in animals is genetically based, and we give examples of features of human language that evolve slowly enough that genetic adaptations to them may arise.

We welcome Christiansen & Chater's (C&C's) bold proposal that "language is easy for us to learn and use, not because our brains embody knowledge of language, but because language has adapted to our brains" (target article, sect. 1, para. 3). Whether our language capabilities derive from a Universal Grammar (UG) or draw on more "domain-general" mechanisms, we believe there is somewhat more potential than C&C want to allow for genetic adaptations to language or language processing.

Modern humans' unique social system makes demands on language unknown in any other species. We are the only animal with complex systems of cooperation and exchange among unrelated individuals. We help people we may never see again; we have an elaborate division of labour; and we sometimes act in ways that benefit the group but at considerable cost to our own fitness, even to the point of causing death. Our social system is one based on reciprocation and trust and is therefore vulnerable to cheats who take advantage of the goodwill of cooperators, without returning aid themselves.

Human language was almost certainly required to manage the social complexity of modern human society (Pagel 2008). Some of the most frequently used words in spoken communication are those relating to "social coordinates" – the pronouns *I*, *you*, *he/she*, *we*, *they*, *who*, and verbs *to say* and *to know*. As language became more sophisticated in our ancestors, so also grew the opportunities to use it for personal gain – to enhance one's reputation, to tell lies, and to spread rumours. Individuals with poor language skills would have been markedly disadvantaged in a society of shrewd, guileful, and self-interested speakers.

It does not matter for our view whether the selective pressures for language and language skills built something like a Universal Grammar or whether they modified elements of a more "domain-general" apparatus (whatever form it may take). If the latter, general traits (such as arms and legs or general cognitive abilities) are typically shaped by competing demands of different functions and environmental contingencies. Our position is that a facility with language would have been one of the key sets of demands shaping some of these domain-general mechanisms.

Bird-song is not a recursive symbolic language, but it illustrates how the foundations for producing a culturally influenced and geographically variable trait may be encoded genetically (Nottebohm 2005). In humans, evidence for genetic variation related to language learning and processing may be all around us. Our brains appear to be "wired for language" (Glasser & Rilling, in press), brain structures related to language are likely to be heritable (Thompson et al. 2001), and people seem to vary greatly in their abilities to express themselves verbally. The pervasive phenomenon of dyslexia, which seems to affect both language learning and production, and the phenomena associated with FOXP2 variants also suggest that genetic variance for language capabilities is common.

C&C argue that language changes too rapidly for genes to get a fix and adapt to it. Possibly, but the human immune system has diverged genetically around the world in response to rapidly evolving parasites. We also note that not all elements of language evolve at a high rate. Dunn et al. (2005) report phylogenetic signals in Papuan language typology that may have been preserved for many millennia. We have shown that highly expressed or frequently used words in the Indo-European lexicon evolve as slowly as some genes (Pagel et al. 2007). The word for the number "two" is highly expressed and is cognate across the entire Indo-European language family. Thus, here is a lexical item that has retained homology throughout roughly 130,000 language-years of evolution. By comparison, a genetic tolerance in adults for lactose probably arose and spread to high frequencies within the last 6,000 years in some populations of this same language family (Burger et al. 2007).

We do not suggest that there is a gene for the number "two." But these examples from empirical studies may indicate that there are general features of linguistic systems that, either on their own or because of their links to other systems, change slowly enough that we could expect to see genetic adaptations for the cognitive mechanisms that process them. The frequency-effect we document also depends on the part of speech. For a given frequency of use, conjunctions evolve fastest, followed by prepositions, then adjectives, verbs, nouns, special adverbs, pronouns, and finally numbers, which evolve very slowly. Why parts of speech influence the rate of evolution is unclear but may be relevant in a very general way to C&C's discussion of Frequency × Regularity interactions. We wonder if, for example, the different parts of speech are linked with (or overlap with) other features of language that may make them less prone to change over time. Alternatively, might the rank ordering of parts of speech correspond to memory and production effects related to word "concreteness" (e.g., Bleasdale 1987; Jessen et al. 2000), with numbers the most concrete and prepositions the least?

We see human language as a trait on which we have stamped our cognitive and psychological signatures along the road to ensuring that language is a useful tool for us. This is, in some sense, the "flip side" of C&C's view of languages as semi-autonomous systems that adapt to us. Some of the signatures of our shaping of language may emerge from historical analyses of the variation among languages. C&C discuss some, and the frequency-effect discussed above may be another. Social factors may also play a role. We have recently been able to show that languages often exhibit a rapid or punctuational burst of evolution around the time of their divergence from a sister language (Atkinson et al. 2008). One interpretation of our findings is that humans use language as a tool for establishing a distinct social identity. If social forces such as this can leave their imprint on languages over historical time, we should not be surprised to find that features of our information processing systems can do the same. Equally, for a trait of such importance to our lives we should not be surprised that we have also adapted to it.

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Language as ergonomic perfection

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Abstract: Christiansen & Chater (C&C) have taken the interactionist approach to linguistic universals to an extreme, adopting the metaphor of language as an organism. This metaphor adds no insights to five decades of analyzing language universals as the result of interaction of linguistically unique and general cognitive systems. This metaphor is also based on an outmoded view of classical Darwinian evolution and has no clear basis in biology or cognition.

For the last five decades, much linguistic research has adopted an interactionist position about the sources for Universal Grammar (UG). This approach partitions overt language universals into those determined by inborn linguistic structures and those shaped by language performance systems (e.g., learning and general cognitive factors). For example,

> Many an aspect of adult . . . linguistic structure is itself partially determined by the learning and behavioral processes that are involved in acquiring and implementing that structure . . . some formally possible structures will never appear in any language because no child can use [or learn] them. (Bever 1970, pp. 279–80)

Christiansen & Chater (C&C) adopt an extreme version of the interactionist approach, eliminating the contribution of linguistically unique genetic bases for language in the brain. Their designated metaphor is language as an organism that has evolved to fit the human brain: "Language is easy for us to learn and use,

not because our brains embody knowledge of language, but because language has adapted to our brains" (target article, sect. 1, para. 3).

Yet, mentioning "the brain" does nothing to enrich or support their claims. Unlike, for example, Deacon (1997), C&C say nothing about *which* properties of the human brain are such that language has adapted to *them*. C&C restate much that has been said before about the influence of behavioral systems, while claiming – without demonstration – that they exhaust the constraints on linguistic universals. The critical claim is that *the individual language learner/user* filters possible languages via general cognitive, communicative, and physiological processes. This is tantamount to the idea that language is a tool, ergonomically shaped to be maximally usable, no different in principle from a Boeing 707 or recipes for Salzbuger Nockerl. Yet no one would reasonably propose that airplanes or recipes are *organisms that evolved* to fit the human brain. C&C suggest that it is the alleged *unconscious* emergence of possible languages that makes language unique from other tools. Perhaps so, but they do not offer any theory of what the brain has to do with this that makes it reasonable to apply the organismic evolutionary metaphor only to language.

Characterizing language as evolving on its own also contributes unnecessary confusion because C&C restrict their notions of evolution to a classic model. For example, contrary to their interpretation, the adaptive complexity of biological organisms only *marginally* arises from random genetic variation, winnowed by natural selection. The many non-selective processes they cite (genetic drift, genetic hitchhiking, epigenetics, etc.), and others (e.g., evolutionary capacitors [Rutherford & Lindquist 1998] and alternative splicing [Blencowe 2006]), suggest that *no* complex organism, never mind language, evolved via selective winnowing of variants in the orthodox Darwinian model. Few biologists today adopt that pristine model, while some go as far as stating that *"natural selection is just one, and maybe not even the most fundamental, source of biological order"* (Gibson 2005; see also Carroll 2001; Sherman 2007; Wagner 2005).

After ignoring many lessons from current models of evolutionary processes, C&C proclaim it "astronomically unlikely" (sect. 4, para. 4) that *non*-adaptationist processes may have produced genuine evolutionary novelties. But, there are many "unlikely" cases in which non-selectionist mechanisms have been pivotal: the evolution of the genetic determination of sex (Quinn et al. 2007), the development of the eye (Sherman 2007), and the adaptive immune system (Hiom et al. 1998). Appraised "likelihood," of course, depends on the probability baseline that one adopts. Given a specifiable genetic configuration, combined with specifiable external and internal factors, the probability is close to one. If the assumed probability baseline is a random swirl of molecules (or a tornado in a junkyard, as Hoyle [1983, pp. 18–19] and Pinker [1997] famously suggest), then indeed the probability of evolving a camera eye, or Universal Grammar – or a Boeing 707 – is vanishingly small. But why should one take anything like that as a relevant baseline?

C&C note further that, "Small genetic changes lead to modifications of existing complex systems … they do not lead to the construction of a new complexity" (sect. 4, para. 5). This statement is false when master genes (homeoboxes) are involved (see, e.g., Ronshaugen et al. 2002; Sherman 2007).

In brief, insofar as one takes seriously "language evolving" as a meaningful metaphor, C&C's archaic view of biological evolution would render their arguments unlikely at best, and, most likely, wrong.

Secondly, the properties of cognition that C&C invoke to explain language occur in other species, including those that are less clearly present (e.g., hierarchical processing; Conway & Christiansen 2001). Why did language not "evolve" in the service of these species? Humans must have innate equipment quite different from those species that also display their version of "general" human traits.

For "language as organism" to evolve under selective pressures enforced by the brain requires a suitable starting point: C&C suggest that a "proto-language" (sect. 7.1, para. 1) could fill the void. They reference computational models of the emergence of compositionality from a proto-language (cf. Smith et al. 2003b), but ignore a critical feature of these models – the agents are equipped with a specific compositional mechanism for grammar induction. Thus, at a bare minimum, the brain must have contributed proto-language and such structural inductive systems as hierarchical processing, and recursion – abilities vastly undeveloped in primates (Conway & Christiansen 2001).

Furthermore, C&C still face the problem of innovation from "proto-langauge." What triggered the first truly structured sentence? The first recursive utterance introduced a transcendentally ungrammatical form. It is mysterious how this structure would ever be produced in the first place, let alone persist in the linguistic pool, if not for some innate capacity. At the very least, a possible pathway for the transition between unidentified cognitive mechanisms is needed, but C&C make no attempt to explicate one.

Finally, C&C report evidence of Broca's area involvement in an artificial grammar task and normal natural language processing (Petersson et al 2004) but omit drastically opposite data (Friederici et al. 2006; Musso et al. 2003).

On language and evolution: Why neo-adaptationism fails

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Abstract: I identify a number of problematic aspects of Christiansen & Chater's (C&C's) contribution. These include their suggestion that subjacency and binding reflect non-domain-specific mechanisms; that proto-language is a "cultural product"; and that non-adaptationism requires overly rich innate structures, and is incompatible with acceptable evolutionary processes. It shows that a fully UG (Universal Grammar)-free version of the authors' neo-adaptationism would be incoherent.

For all linguists who do not view language as a Platonic object, it should be uncontroversial that there is a "fit" between language and the brain (as expressed in Chomsky [1986], where Chomsky introduces his notion of I-language). The common goal is to find out how they fit, and to what extent our cognitive system is dedicated to language.

Christiansen & Chater (C&C) argue that no part is dedicated to language. In brief, that there is no Universal Grammar (UG). This is a strong position that deserves extensive research, taking into account the properties we know language possesses (the derivation of condition B, in Reuland 2005b, illustrates what this involves). How well, then, do the authors succeed?

C&C focus on what they call "abstract" properties (see sect. 2) and discuss two such properties to establish initial plausibility. One is subjacency (Chomsky 1981). C&C argue that subjacency is not specific to language, but derivable from general processing constraints (sect. 6.3) or, possibly, "cognitive limitations on sequential learning" (sect. 7.2), referring to Berwick and Weinberg (1984) and Ellefson and Christiansen (2000) in this regard. Subjacency effects are real. But we know by now that restrictions on extraction result from a variety of factors (see Szabolcsi [2005] for a state-of-the-art overview; and see, e.g., Khomitsevich [2008] for cross-linguistic variation in island effects). Subjacency is not a primitive. The nature of the resources for language processing is still open, and more may be involved

than just general working memory (see Reuland [forthcoming], elaborating on Ullman [2004] and Baddeley [2007]). Even granted C&C's conception, the experiment in Ellefson and Christiansen (2000) does not bear on subjacency: nothing forces a forbidden extraction. The other issue C&C bring up is binding (discussed further on).

The main line of the article takes a different tack: The assumption of an innate UG leads to a logical problem of language evolution. C&C argue that the emergence of a dedicated language system/UG can neither be explained by adaptationist (Pinker & Bloom 1990), nor by non-adaptationist mechanisms. Hence, they conclude, there must be a third way: no UG and "language *is* shaped by the brain" (emphasis added).

Their discussion gives the paradoxical impression that C&C, though cognitive scientists, espouse a Platonistic view of language: an object external to the mind, which evolves and adapts to the latter; a view I characterize as *neo-adaptationism*. Note that C&C just assume that "functional" principles are domain-general, whereas only a moment's reflection shows that there is nothing "natural" in the way salience, topicality, and so on, are encoded in natural language (Slioussar 2007). Isn't there a great rhetorical tradition in which what is most important comes last?

C&C reject the non-adaptationist position, positing that non-adaptationists postulate overly rich innate structures. But, in view of the Minimalist Program (Chomsky 1995) and the approach to evolution in Hauser et al. (2002), this is incorrect. No more is required than a finite set of vocabulary items (lexical and functional), a combinatory operation of (external and internal) Merge plus associated interpretive operations, a checking operation (comparing the feature contents of elements), and locality conditions in operations. These show up in the form of restrictions on "attractors" for movement ("phase heads" in current terminology) and in the form of restrictions on the domain where attractors can find their targets. All this is close to what C&C would have to assume anyway (also construction grammar does not allow dispensing with combinatory principles, unless to the penalty of incoherence).

What is problematic in C&C's presentation is that (1) they do not make clear what language is, and – not surprisingly, given (1) – that (2) they don't discuss how language is encoded; and (3) that, although they claim that "linguistic adaptation allows for the evolution of increasingly expressive languages" (sect. 5, para. 1), C&C say nothing about what it means for one language-stage to be more expressive than another, and what discontinuities must be involved.

For reasons of space, I focus on signs here and argue that even their evolution involves more "UG" than meets the eye. I start with C&C's characterization of the initial state, proto-language, as a "cultural product likely to be highly variable over both time and geographical locations" (sect. 2, para. 7). But even so, language must be a product of the mind, not an external object that emerged by miracle.

Such a proto-language minimally stands for a collection of Saussurean signs, conventional pairings $< f, i >$, where *f* is a form in a medium (sound, gesture) and *i* its interpretation as a concept (see Saussure 1916). The term "cultural" glosses over a crucial issue. The pairings themselves may be culturally determined, but the fact they are possible cannot be. Even a neo-adaptationist must assume an evolutionary discontinuity here. The same applies to arbitrariness of pairings. Arbitrariness is a yes-no property. It can only emerge by a discontinuity. By its very nature, it must be dedicated to language, hence reflect UG as commonly understood. So, even on their own terms, C&C are committed to a minimal UG.

But more is at issue here. C&C leave open whether their proto-language allows free combination of signs. However, free combinability – recursion – must develop at some point. Recursion minimally requires concatenation, combining two objects into an object of the same type, which is in turn available for concatenation. This entails that linguistic signs must be triples of the general form in (1) shown below, rather than pairs.

1. $< f, g, i >$

with *f* and *i* as explained above and *g* a formal instruction driving the computation.

The addition of *g*, as a formal instruction representing combinability, leads us beyond the Saussurean sign. It is a *minimal* change, but *qualitative* in nature. Adding this slot to the sign frees the way for (varying) grammatical operations. Free combinability requires a concomitant *interpretive* operation, determining the interpretation of a complex element in terms of the interpretation of its parts.

A different change is needed for signs as abstract mental objects, as in Example (2) shown below:

2. $< c_f, g, c_i >$

where c_f and c_i are "formal" mental encodings of instructions for the language-external systems of realization and interpretation.

This feature is needed for planning, embedded recursion, and handling dependencies (see Reuland 2005a; in press). Such items are not simple signs anymore, but instructions to form signs. Forms and concepts may reflect culture, but the ability to form such pairings does not. This ability involves, again, a qualitative change, incompatible with neo-adaptationism.

Human language has many further characteristic properties. Take Example (3), shown below, where *he* cannot be valued as *no one*, since *no one* cannot denote an individual.

3. *No one* has a gun. *Will *he* shoot? (the asterisk here indicating ill-formedness)

But *he* can depend for its interpretation on *no one* in Example (4):

4. *No one* was convinced that *he* would be welcome.

Example (4) exhibits binding, that is, *interpreting an expression in terms of another expression*. Again, this is a yes-no property, not subject to gradation. Binding is a core feature of language as we know it (see Reuland, under contract). Binding transcends culture and pragmatics. Its emergence involves a discontinuity that has to be encoded in the system itself, and hence, reflects UG. Such discontinuities are a challenge for any neo-adaptationist approach, but fascinating to investigate nonetheless.

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Language acquisition recapitulates language evolution?

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Abstract: Christiansen & Chater (C&C) focus solely on general-purpose cognitive processes in their elegant conceptualization of language evolution. However, numerous developmental facts attested in L1 acquisition confound C&C's subsequent claim that the logical problem of language acquisition now plausibly recapitulates that of language evolution. I argue that language acquisition should be viewed instead as a multi-layered construction involving the interplay of general and domain-specific learning mechanisms.

In section 8.1 of the target article, Christiansen & Chater (C&C) suggest that phylogeny (how language evolved in the species over time) begets ontogeny (developmental properties of day-to-day learning by the child), inferring that certain underlying mechanisms for these very different processes are the same. Focusing

on L1 acquisition, I argue that the authors' elegant conceptualization and simulations of the logical problem of language evolution do not necessarily translate to the untidy developmental facts of language acquisition in the current linguistic environment. Specifically, it may be premature on C&C's part to advocate general-purpose cognitive mechanisms alone to explain child language learning and the repertoire of rule types that governs it.

As a first step, terms such as "language-specific constraints" and "general-cognitive constraints" must be regarded with caution. While domain specificity is often readily identified, domain generality is frequently a "moving target," precisely because it is definable by degree. That is, we say that a mechanism is domain-specific so long as it only does what it evolved to do, or as long as it is only used for learning within its domain. But we can only say that a mechanism is *more or less* domain-general: It is more domain-general or neutral the more it generalizes to other tasks outside its domain. In principle, this effect may not be problematic – after all, lots of phylogenic and ontogenic distinctions involve matters of degree. In synchronic terms, any general mechanisms of cognition do not dispense with the specific ones; instead, the existence of general machinery presupposes the existence of functionally related specific mechanisms. When dealing with the countless complexities of linguistic structure, Skinner's box cannot afford to be empty: it must at least contain a random assortment of various entities (paraphrasing Satterfield & Saleemi 2003). In other words, the basis from which L1 development commences had better be minimally equipped to supply learners with knowledge of grammatical functions, and Case systems, and so on, just in case children encounter these properties in their primary linguistic data.

Second, C&C state that

> if language is viewed as having been shaped by the brain, then language learning is by no means a standard problem of induction . . . instead, the task is simply to give the same answer as everybody else – because the structure of language will have adapted to conform to this most "popular" guess. (sect. 8.1, para. 2)

This view has several consequences in the developmental context that are not easy to explain. Consider the following cases: (1) Children in American English-speaking environments are widely attested to omit subject pronouns in tensed clauses (e.g., *Toys in there*; Hyams 1986). (2) They also insert an extra *wh*-expression in long-distance questions: for example, "What do you think *what* pigs eat?" (Crain & Thorton 1998). The structures in question seem to be at odds with "everybody else" – for example, with adult English, which contains no such features (although these are by no means "wild guesses," since in the former case [1], languages like Standard Spanish and Italian pattern somewhat in this way; and in the latter case [2], certain German dialects would be appropriate). However, it would be computationally "easier" to simply have a zero or deleted Complementizer in this site, rather than the *wh*-word. These tokens beg the question of why children should exhibit such tendencies at all. Perhaps the task requires children to initially exert multiple types of "biases" in order to obtain the maximal advantages of the grammar (Gawlitzek-Maiwald & Tracy 2005; Roeper 1999; Saleemi 2002; Satterfield 1999a; 1999b; Yang 1999; 2002).

On common ground with C&C, it is doubtful that a highly language (domain)-specific Universal Grammar (UG) functions as the sole machinery in the child's task of language acquisition. However, this position need not exclude the possibility that children pick which apparatuses they use, more-generalized or less-generalized tools, and to what degree, in a flexible and adaptive manner. Keeping this postulation in mind, consider the critical period in L1 acquisition. It has been successfully argued that not all aspects of language display critical period effects. Specifically, the acquisition of lexical items, the concatenation of words, and the nuts and bolts of semantically based principles of word order seem immune to age-related "atrophy" of language acquisition (Hudson & Newport 1999; Jackendoff 2002; Sorace 2003). However, the capacity to acquire other parts of language in late language learning, such as the inflectional system or real intricacies in phrase structure, appears to be largely diminished (Lardiere 1998; 2000). These common L1 versus L2 conditions become at once isolatable by viewing language acquisition as a multi-layered construction with distinct learning mechanisms.

Ultimately, the solution to the logical problem of language acquisition may reside in the possibility of possessing several initial knowledge states in which domain-general mechanisms interact with domain-specific components designed to acquire the most arbitrary and least systematic knowledge of the target grammar. States that stabilize over several progressive stages could then emerge, with the help of additional domain-general learning mechanisms, which handle increasingly more systematic principles of the grammar. In sum, each transitional state may be shaped by the myriad effects of learning, or, more appropriately, of acquisition, which can be viewed as the combination of experience and internally determined processes such as maturation, learning mechanisms, and language-specific computations.

The brain plus the cultural transmission mechanism determine the nature of language

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Abstract: We agree that language adapts to the brain, but we note that language also has to adapt to brain-external constraints, such as those arising from properties of the cultural transmission medium. The hypothesis that Christiansen & Chater (C&C) raise in the target article not only has profound consequences for our understanding of language, but also for our understanding of the biological evolution of the language faculty.

Christiansen & Chater (C&C) provide a thought-provoking account of language as a cultural adaptation to the minds of language learners: Language evolves through repeated cultural transmission, adapting to multiple pressures impinging upon its learning, representation, and use. This strikes us as a powerful explanatory framework, and we hope the target article will stimulate more work fleshing out the precise relationship between constraints on language arising from the brain and features of linguistic structure.

In fact, we believe that there are two respects in which the target article actually understates the full implications of this hypothesis. First, C&C focus on language as an adaptation to language learners' brains – but language must also adapt to constraints external to the human mind. Second, in discussing their account's implications for understanding biological evolution, C&C point out the "moving target" problem – but there are at least two further issues with the interaction of cultural and biological evolution they do not recognize. Taken together, these completely change the viability of accounts based on the adaptive

evolution of a strongly constraining, domain-specific biological faculty for language.

Although there are, of course, fundamental differences between the account offered by C&C and the Universal Grammar (UG) account they contrast it with, it is useful nevertheless to focus on a point of similarity: Both argue that language is how it is because the mind forces it to be so (the crucial difference being the extent to which the relevant mental components are domain-specific or domain-general, and who does the fitting to what). Both postulate a good fit between observed properties of language and properties of the human mind: if we see some linguistic property in the world, we can reasonably infer that it reflects a property of our minds.

We have previously demonstrated, however (Kirby 1999; Kirby et al. 2004), that mental properties cannot simply be read off from language universals, because the cultural process mediating between aspects of the mind and features of language distorts the underlying biases of human learners. For example, culture can amplify weak biases to give strong universal effects. This means that cultural transmission can obscure underlying differences in mental structure: for example, strong universal tendencies towards regularity can result from various levels of preference for regularity in individual learners, and (in extreme cases) the same observed distribution of languages can result from learners with widely differing strengths of preference for regularity (Kirby et al. 2007).

This suggests that, while we can probably get an idea of the general flavour of the human mind from observable linguistic properties, making specific inferences is more risky. To draw appropriate conclusions from a given distribution of languages, we must understand the rather opaque relationship between mental properties and linguistic properties resulting from cultural transmission.

Furthermore, not all pressures acting on language during its transmission are mental: language is not only well adapted to its users' brains, but also to its medium of transmission. Computational modelling work highlights the importance of the *learning bottleneck*: learners must infer the structure of an infinitely large language from a finite subset. This bottleneck introduces a pressure for generalisation to which language must adapt, for example, by becoming compositional (Kirby 2001; Smith et al. 2003a). Importantly, the bottleneck is not a property of language learners' brains, but rather of the medium through which language is transmitted, namely, a finite dataset. Linguistic properties that are eminently learnable (and therefore well adapted to the brain) may be disfavoured due to this transmission factor, or vice versa. Consequently, linguistic features represent a product of, or a compromise between, several pressures acting on language transmission, some (but not all) of which reside in the human brain.

There are therefore good practical reasons for taking cultural evolution seriously. However, cultural evolution is more than just a methodological hassle for cognitive scientists: the same arguments radically alter the plausibility of scenarios for the evolution of the language faculty. C&C point out one problem for biological evolution, which arises from cultural transmission – evolution is chasing a moving target. We raise an additional problem: Given the opaque relationship between mental and linguistic features, much of the human biological capacity for language will be *shielded* (Ackley & Littman 1992) from evolution. For example, Kirby et al. (2007) show that the strength of prior preferences for particular structures in language arising from an individual's biology may have no effect on the strength of the resulting universals. Under this scenario, selection is completely blind to the strength of the prior biases of individuals and there is no selection for nativisation, nor for stronger, "more desirable" prior preferences for certain languages (Smith & Kirby 2008).

Furthermore, cultural transmission may actually hinder the evolution of a priori functional domain-specific features of the language faculty: Evolving biases for communicatively functional languages is problematic for culturally transmitted languages, because the biases of individual learners require a critical mass of learners and a reasonable span of cultural time to make their advantageous properties felt (Smith 2004). Indeed, based on such models, we expect that practically the only scenario under which biological evolution will favour particular language-learning predispositions is when those predispositions are domain-general, and selected for on account of their less problematic (acultural, non-linguistic) applications. While this is entirely consistent with C&C's argument, we believe it also follows naturally from taking cultural evolution seriously.

So if evolving a functional domain-specific set of language biases is problematic, how can we best understand the evolution of the human faculty for language? C&C force us to revisit the human uniqueness of language from a comparative perspective, and (we suggest) pose a fascinating, important new challenge for evolutionary biology: Which of their suggested domain-general pressures responsible for shaping language are unique to humans, and what can this tell us about the evolutionary origins of the species-unique trait of language? Are there pre-adaptations for the cultural transmission of linguistic systems (e.g., vocal learning capacity; intention-sharing ability)? If so, how much linguistic structure naturally falls out of the cultural transmission process once these pre-adaptations are in place?

Case-marking systems evolve to be easy to learn and process

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Abstract: Christiansen & Chater (C&C) suggest that language is itself an evolutionary system, and that natural languages "evolve" to be easy to learn and process. The tight economy of the world's case-marking systems lends support to this hypothesis. Only two major case systems occur, cross-linguistically, and noun phrases are seldom overtly case-marked wherever zero-marking would be functionally practical.

All languages employ some morphosyntactic means of distinguishing the core noun phrase (NP) arguments within a clause. The two basic predicate types are intransitive and transitive verbs, giving three core grammatical functions: S indicates intransitive subjects (*The girl slept*); A, "agent" of a transitive verb (*The girl saw a pig*); and P, "patient" (*The girl saw a pig*). Some languages (e.g., Chinese, English) distinguish A and P using word order: thus, we know which mammal saw which, because A always precedes the verb and P follows.

However, many languages employ case-marking to distinguish A and P, as in Latin:

1a. Puella venit.
girl.(NOM) come.PRES.3SG
"The girl comes."

1b. Puella puer-um audit.
girl.(NOM) boy-ACC hears.PRES.3SG
"The girl hears the boy."

1c. Puella-m puer audit.
girl-ACC boy.(NOM) hear.PRES.3SG
"The boy hears the girl."

Since S (intransitive subject) never co-occurs in a clause with either A or P, it needs no unique marking. Conversely, A and P always co-occur, and therefore must be marked differently to avoid confusion. Assuming a resolution of the tension between speaker effort (only produce essential morphemes) and listener comprehension (keep potentially ambiguous forms distinct), there are two major solutions. To distinguish A and P morphologically, it is most economical to either group S and A together, using the same case-marking for both, or else group S and P together, again using the same case for both.

These groupings, maximizing economy and comprehensibility, are exactly what we find: only two major morphosyntactic systems occur in the world's languages. The "accusative" system groups all subjects together (nominative), as opposed to all objects (accusative), as in Latin, Turkish, and Japanese, giving an [SA][P] pattern. Conversely, the "ergative" system groups intransitive subjects and objects together (absolutive case), as opposed to transitive subjects (ergative), giving an [SP][A] pattern. Here is an illustration of this from the Australian language Yalarnnga (taken from Blake 1977):

2a.	ngia	wakamu	
	me.(ABS)	fell	
	"I fell."		
2b.	nga-tu	kupi	walamu
	me-ERG	fish.(ABS)	killed
	"I killed a fish."		
2c.	kupi-ngku	ngia	tacamu
	fish-ERG	me.(ABS)	bit
	"A fish bit me."		

Strikingly, languages rarely mark *each* of the three core functions; clearly, only one member of the opposition needs overt marking. We therefore usually find a morphologically unmarked case: in the accusative system, the SA grouping (i.e., nominative), and in the ergative system, the SP grouping (i.e., absolutive). Thus, in the Latin examples, only accusative P has an overt suffix, while nominative SA is unmarked; and in Yalarnnga, only ergative A has a case suffix, while absolutive SP is unmarked (the parentheses in the [1] and [2] examples shown earlier indicate this null case morphology on SA and SP, respectively). In both systems, the unambiguous argument S is typically unmarked, again maximizing economy and clarity.

Both the accusative and the ergative systems are widespread, among languages which are really and genealogically diverse. Clearly, humans are not genetically adapted for one or the other system; moreover, since these are the major, but not the only systems that occur cross-linguistically, it would be incoherent to suggest that they are parametrized. It seems reasonable to conclude, then, that *languages* have generally adapted to maximize learnability and economy by utilizing the major systems.

Logically, other possible alignments of A, S, and P exist. For instance, [AP][S] marks A and P in the same way, but S differently; this, however, would set up exactly the confusion between A and P, which the major attested systems neatly avoid. This system occurs in a restricted set of pronominals in some Iranian languages; however, Comrie (1989, p. 118) notes that it is not stable, instead representing the change from an earlier ergative system to an accusative system. Such marking is unattested for core NPs. Since it does not occur, it is most likely unlearnable – hardly surprising, since it is dysfunctional.

Three broad possibilities remain. First, a tripartite system consistently uses a distinct form to mark each of A, S, and P. This lacks the economy of the two major attested systems, and is vanishingly rare. One or two Australian languages are reported as having a tripartite system for all NPs: Warrungu (Comrie 2005) and Wangkumara (Breen 1976). Clearly, this system *is* learnable, but is strongly dispreferred by human learners; as predicted, then, languages have generally not adopted this system. Second, a neutral system would not differentiate between A, S, and P at all, either by position within the clause, case-marking, or head-marking (i.e., verbal morphology indicating the person/number of the core arguments). Although this occasionally occurs, in a very restricted manner, for pronominals (Comrie 2005), it is again unattested as a system for marking core NPs, and is thus, we can speculate, unlearnable. The third possibility is the split-S, or active system, which case-marks S (intransitive subjects) differently according to whether they are semantically agents or patients. This case system does occur, but is cross-linguistically rare (Blake 2001, p. 124), arguably, again, because it lacks the economy of the two major systems.

Mixed systems, however, occur frequently. Both major systems exhibit DIFFERENTIAL CASE-MARKING (see Jäger 2007), meaning that NPs receive different – or zero – marking according to their position on a hierarchy of animacy and/or definiteness, sketched in Example (3) below (Blake 2001, p. 137):

3. 1st person pronoun > 2nd person pronoun > 3rd person pronoun > proper noun > full NP

Accusative languages typically mark P overtly only towards the top of the hierarchy; English has case distinctions for a subset of pronouns (*I/me*, etc.), but none for full NPs. In fact, accusative languages nearly always have differential object-marking (Blake 2001, p. 119). P arguments lower on the hierarchy are zero-marked, while higher ones are overtly accusative. Conversely, ergative systems work upwards, typically confining overt ergative marking to full NPs, or a subset thereof: Blake (2001, p. 192) notes that the Australian language Mangarayi marks ergative only on inanimate nouns, lowest on the hierarchy. In both systems, restricting overt marking to a subset of arguments achieves greater economies. Interestingly, most ergative languages are actually "split ergative," often marking NPs high on the hierarchy (pronouns) by the accusative system, but lower NPs as ergative. This alignment may appear difficult to learn, but Jäger (2007) demonstrates, using evolutionary game theory, that split ergative is actually highly efficient and stable, and fully functionally motivated.

Finally, case-marking and head-marking often co-occur within a language as grammatical function-signalling strategies for core NPs. Crucially, though, these strategies typically conspire, ensuring that no function is marked twice: a case/agreement hierarchy has subjects at the top (generally signalled by verb agreement) and indirect objects and other non-core NPs at the bottom (often signalled by case). This is another highly efficient system, and again illustrates the way languages apparently evolve to be learnable.

Language as shaped by the brain; the brain as shaped by development

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Abstract: Though we agree with their argument that language is shaped by domain-general learning processes, Christiansen & Chater (C&C) neglect to detail how the development of these processes shapes language change. We discuss a number of examples that show how developmental processes at multiple levels and timescales are critical to understanding the origin of domain-general mechanisms that shape language evolution.

Christiansen & Chater (C&C) argue that language is shaped by the constraints of the brain, and that, over time, language changes to fit those constraints. They demonstrate the implausibility of an innate Universal Grammar (UG) that encodes arbitrary principles of language, and suggest that the features of language we observe are those best suited to the domain-general constraints humans bring to the problem of language acquisition. Both the innate UG that C&C reject and the domain-general constraints that they propose are thought to arise through evolution – they are encoded in the genome. However, genes do not function in isolation from their environment, and domain-general learning mechanisms do not exist in the absence of external input (see, e.g., Spencer et al., in press). Therefore, understanding the mechanisms that shape language change involves understanding how domain-general processes are shaped by the interaction of genes and environment. This interaction is tied to development over multiple timescales. Research suggests that even domain-general processes, like those C&C outline, change over the course of in-the-moment learning and developmental time. Unless we provide an explanation of language evolution with respect to developmental process, we have done little more than substitute one set of genetically encoded principles for another.

Interactions occur at multiple levels, from gene expression and cell signaling to the formation of neural networks and behavior (Tomblin & Christiansen, in press). The rise of molecular genetics has greatly changed how we investigate cognition, neurodevelopment, and behavior. At present we understand very little about how genes are involved in these processes. However, we do know that genes make regulatory factors and signaling molecules that interact in highly complex frameworks, modulated by environmental influences, to build and maintain the brain. These processes can have an impact on the nature of domain-general learning mechanisms that may drive language change. For example, brain-derived neurotrophic factor (BDNF) is a protein that is important for synapse formation, and, in particular, modulates hippocampal learning. Egan et al. (2003) found that BDNF polymorphisms are associated with differences in verbal episodic memory. Given that language learning is reliant upon long-term storage of arbitrary mappings, BDNF is widely believed to contribute to vocabulary learning. Thus, inheritance of a particular polymorphism may influence word learning abilities. At the cellular level, secretion of BDNF leads to changes in neurotransmitter activity, synaptic connectivity, and long-term potentiation (LTP). In addition, external stimulation that produces LTP influences the expression of BDNF (Patterson et al. 1992). Thus, the interaction between genes, their expression, and the environment is critical for determining the properties of learning systems relevant to language.

At higher levels, we see evidence of complex interactions in the development of domain-general capacities. MacDonald and Christiansen (2002) demonstrated this in a neural network that was trained to predict the next word in a sentence. Performance in this task is dependent on the network's processing capacity for word sequences. Their simulations showed that processing capacity is an emergent property dependent on both the architecture of the network and its experience. Similarly, Ross-Sheehy et al. (2003) showed that 4-month-olds have a visual short-term memory capacity for only one object, whereas by 13 months, infants' capacity increases to four objects. Thus, infants are not born with an adult-like short-term memory. Rather, this capacity depends on developmental processes and is likely to be modulated by biological and environmental factors. Those factors include the way memory representations are brought to bear on in-the-moment behavior; Spencer et al. (2008) have shown that the visual working memory capacity of preschoolers depends on the specifics of how memory representations are probed. This provides evidence of change in domain-general processes at the level of the in-the-moment timescales from which learning and development emerge (see also, Samuelson & Horst 2008).

How might developmental changes in these domain-general mechanisms impact language processing? We know that age and previous linguistic experience influence the process of language acquisition and that there are large differences in the ability of children and adults to learn language. Acquisition of a first language is accomplished with relative ease; in fact, children are remarkable language learners. Second language acquisition as an adult, however, is quite difficult. One way to explain this difference is to consider the different developmental histories children and adults bring to the problem of learning a language. If developmental history affects future learning, we might suppose that information learned earlier will be weighted more heavily than information learned later. Under this assumption, adults will have difficulty learning a new language because of their developmental history (i.e., they assign less weight to new information given previous language experience). Even though adults and children bring the same domain-general learning constraints to the problem, differing developmental histories can affect their ability to learn a language.

Experimental work by Hudson Kam and Newport (2005) has demonstrated that developmental history can impact the learning processes that shape language change. When adults and 5- to 7-year-old children were exposed to an artificial language with an inconsistent grammar, the children regularized the language, producing more consistent constructions than the ones they had heard, while the adults produced only the constructions they had heard. Hudson Kam and Newport hypothesized that this difference in regularization is caused by differences in the way children's and adults' learning processes are constrained by prior developmental history. Thus, the temporal aspect of development, that is, that children have less accumulated developmental history, can have an impact on how languages will form and change over time.

These examples demonstrate that development is essential for describing the learning processes that drive language acquisition and language evolution. Factors that determine the learnability and expressivity of language are shaped by developmental history. This history is determined by an interaction between an organism and its input and between genes and the environment at multiple timescales. Therefore, we agree with C&C that language has changed to fit the brain. However, in order to understand how language changes, we must also understand how it develops in the individual.

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Language is shaped for social interactions, as well as by the brain

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Abstract: Language learning is not primarily driven by a motivation to describe invariant features of the world, but rather by a strong force to

be a part of the social group, which by definition is not invariant. It is not sufficient for language to be fit for the speaker's perceptual motor system. It must also be fit for social interactions.

Christiansen & Chater's (C&C's) target article is a clear and thought-provoking presentation of the many inconsistencies within and between various versions of the Universal Grammar (UG) theory. One of the clearest examples of such inconsistencies, which is not directly touched upon in this article, is the question of what happened to the original "poverty of the stimulus" argument (Chomsky 1980), claiming that language simply cannot be learned with the ease and speed observed in children without help from a genetic source. This argument is crucial for upholding any kind of theory about a UG. Without it, the pressure for a genetic component in language disappears. However, cleverly avoiding many of the earlier inconsistencies, the Minimalist Program (e.g., Hauser et al. 2002) only maintains that rules for recursion are innate, thereby leaving at least 99.9% of all language content to be learned. This is paradoxical. Why is this rule impossible to learn, if the rest can be learned, and vice versa?

We therefore welcome a theory of language which emphasises the close relationship between linguistic utterances and the content that they represent (e.g., along the lines of Talmy 2000). The pairing of language and meaning in the brain, in the most simple case of direct referencing, probably happens through synchronous firing of auditory and visual cortices (Hebb 1949). Without prior knowledge to guide understanding, these activations will probably spread throughout association cortices along the major fibre pathways; and wherever these two "streams" of information meet, an association is likely to be encoded. This means that linguistic representations are likely to be stored in regions overlapping with or contiguous to perceptuo-motor processing regions (Shallice 1988). Evidence for this line of thinking has been brought forward in relation to action words in premotor cortex (e.g., Hauk et al. 2004) and/or temporal cortex contiguous to V5/MT, a region selective for visual motion perception (Noppeney 2004; Wallentin et al. 2005), spatial relations in posterior parietal cortex (Mellet et al. 1996; 2002; Wallentin et al. 2006; in press), and perspective taking in the frontal eye fields (Wallentin et al. 2008).

With this said, it remains an open question the extent to which the "cognitive system" is a stable unit, or whether it is also open to the influence of language/culture. Even language tied to the most "basic" cognitive operations, such as spatial processing (Levinson 2003) and colour detection, shows a wide spectrum of variation across cultures.

This is not to say that the cognitive system does not constrain language learning at all, but that cognitive processes are themselves subject to the effects of learning. Effectively, what we see is that both language and the cognitive system adapt to each other to a certain degree, even in the case of spatial processing (e.g., Levinson 2003) and colour categorisation (e.g., Gilbert et al. 2006; Winawer et al. 2007). What results in the case of colour categories are "near-optimal divisions" of colour space (Regier et al. 2007). But why not an optimal division? Given the speed of language evolution and the strong innate bias towards certain focal colours, due to the anatomy of the colour-sensitive photoreceptors in the retina (e.g., Bear et al. 2001), why would there be any variation at all? The answer to this question points towards something crucial in language learning, namely, that the motivation to learn a language is probably not primarily driven by a motivation to learn about invariant features of the world, but rather by a strong force to be a part of the social group/society, which by definition is not invariant.

When thinking about language as a system that adapts to constraints imposed by the brain, it is probably important, therefore, to distinguish between language evolution directed towards enhancing fitness in the face of the learner's perceptuo-motor system and language evolution directed towards enhancing language fitness in relation to social dynamics. Where the former is driven by an optimisation of "rational" perceptual/linguistic referencing of the exterior world, the social optimisation will mainly be based on social reinforcement markers. These markers may be proto-linguistic signs, such as facial expressions, or they may themselves be linguistic utterances, giving room for a "run-away" effect, known from sexual selection (Fisher 1999). In other words, socially endowed linguistic changes may happen very fast and to a certain extent be orthogonal to those imposed by the perceptual/linguistic referencing system.

Authors' Response

Brains, genes, and language evolution: A new synthesis

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Abstract: Our target article argued that a genetically specified Universal Grammar (UG), capturing arbitrary properties of languages, is not tenable on evolutionary grounds, and that the close fit between language and language learners arises because language is shaped by the brain, rather than the reverse. Few commentaries defend a genetically specified UG. Some commentators argue that we underestimate the importance of processes of cultural transmission; some propose additional cognitive and brain mechanisms that may constrain language and perhaps differentiate humans from nonhuman primates; and others argue that we overstate or understate the case against co-evolution of language genes. In engaging with these issues, we suggest that a new synthesis concerning the relationship between brains, genes, and language may be emerging.

R1. Introduction

In our target article, we argued for a number of potentially highly controversial theses concerning the relationship between human language and the cognitive and neural systems that support it. Our starting point was Chomsky's (1965; 1980) bold proposal that a core concept in linguistics and biology is Universal Grammar (UG). This species-specific innate endowment comprises a set of universal properties that allow language to develop in the mind of the child in the same biologically determined fashion that a chicken grows its wings. Crucially, the properties of UG are construed as being arbitrary, that is, as having no motivation in terms of how language functions (e.g., as a system for communication). It is from this perspective that Chomsky sees linguistics as, first and foremost, a branch of biology – because the nature of UG is presumed to characterize, albeit at a high level of abstraction, the structure of the brain mechanisms involved in language acquisition (and to a lesser extent, language processing).

UG therefore provides an explanation of the apparently neat "fit" between the structure of human languages and the processes of language acquisition. Children are able to find the "right" linguistic regularities, even in the face of linguistic data that might seem noisy and partial (according to the "poverty of the stimulus" [POS] argument; Chomsky 1980), because the "right" linguistic properties are genetically built-in, as part of UG.

The Chomskyan viewpoint constitutes an extremely strong hypothesis concerning the nature of language development, and has attracted considerable controversy (e.g., Bates & MacWhinney 1987; Pullum & Scholz 2002; Seidenberg 1997; Tomasello 2003; 2004). It is also a strong hypothesis concerning the brain basis for language and its genetic underpinnings, and here too there has been much debate (e.g., Clark & Misyak, in press; Elman et al. 1996; Müller, in press). While UG may be challenged on either of these grounds, or, indeed, concerning whether it provides the right type of theoretical framework for understanding purely linguistic data (e.g., Croft 2001; Goldberg 2006; O'Grady 2005), we argued that the UG approach runs theoretically aground when faced with *the logical problem of language evolution*[1]: that there is no credible account of how a genetically specified UG might have evolved.

Any genetically based biological structure can arise from two types of process: either through a process of (more or less) gradual adaptation driven by selection pressure, or through some non-adaptationist process, by which the structure emerges by "accident." In the target article, we argued that neither story is viable for UG as conceived in Chomsky's framework. An adaptationist account of UG cannot work, because language change is typically presumed to be far more rapid than genetic change. Hence, the linguistic environment is a "moving target," which changes too quickly for a genetically based UG to track. We also pointed out that the spread of human populations creates a further problem. If the adaptationist story is correct, each subpopulation would be expected to adapt to the local linguistic environment, resulting in different UGs across different populations. But such a conclusion contradicts the assumption that UG captures universal properties of human language. Finally, we argued that the non-adaptationist viewpoint is ruled out because the coincidence required to accidentally construct a system of the intricacy and subtlety of UG is too extreme to be credible, according to a simple information-theoretic argument.

The target article put forward a different theoretical viewpoint, which is challenged, amplified, and explored in the highly stimulating commentaries to the article. In particular, we suggested that the fit between language learners and the patterns observed in human languages – a fit which appears to be required to explain how language learning is possible – does not arise because languages are shaped by an innate UG, genetically hardwired in the learner's brain. Instead, this fit arises because languages themselves have adapted to be readily learned and processed. Rather than construing the world's languages as fixed and asking how they are learnable, we proposed that it is more appropriate to consider languages as evolving systems, which have many common patterns in part because they have adapted to common selectional pressures from human learning and processing mechanisms. From this viewpoint, the focus on the genetic basis for language shifts from the search for genes underpinning linguistic constraints, to understanding the pre-existing neural and cognitive machinery on top of which the cultural construction of language was possible.

In responding to the commentaries here, we suggest that this viewpoint can be seen as part of a new theoretical framework for understanding the relationship between brains, genes, and language. We divide our discussion into four broad, although interrelated, themes:

1. *Rethinking classical UG*. The commentaries, and the wider current literature, indicate that theorists – except for a few holdouts (**Harnad**) – are either working outside (**Goldberg**; **Hurford**), or at minimum substantially reconceptualizing, the classic UG framework (**Barrett, Frankenhuis, & Wilke** [**Barrett et al.**]; **Piattelli-Palmarini, Hancock, & Bever** [**Piattelli-Palmarini et al.**]; **Reuland**; **Satterfield**). Somewhat to our surprise, there is relatively little argument to the effect that an evolutionary account can be offered for anything like classical UG. Nonetheless, the commentators raise a range of important issues concerning the possible innate basis for language.

2. *Too much emphasis on the brain*? The issue here is: How far can cultural learning of a system for communication explain language structure, independent of cognitive and neural constraints? Some commentators focus on the explanatory power of learning mechanisms (**Catania**), while others emphasize the mechanisms of cultural transmission (**Blackmore**; **Caldwell**; **Smith, Kirby, & Smith** [**Smith et al.**]).

3. *The biological and cognitive basis for language*. A diverse range of forces are identified, by which language may have been shaped by the brain and beyond (**Aronoff, Meir, Padden & Sandler** [**Aronoff et al.**]; **Behme**; **Brooks & Ragir**; **Corballis**; **de Ruiter & Levinson**; **Dessalles**; **Enfield**; **Fauconnier & Turner**; **Goldberg**; **Greenfield & Gillespie-Lynch**; **Landauer**; **Lieberman**; **Namy & Nygaard**; **Tallerman**; **Toscano, Perry, Mueller, Bean, Galle, & Samuelson** [**Toscano et al.**]; **Wallentin & Frith**). These proposals can also be viewed as providing a range of potentially complementary perspectives concerning what crucial neural or cognitive structures differentiate humans from nonhuman primates.

4. *When can genes and language co-evolve?* The target article makes a narrow argument: that a co-evolutionary, adaptationist account of the origin of a genetic basis for *arbitrary* linguistic constraints (as postulated in UG) is not viable. A range of commentators consider whether the assumptions of this argument apply, especially in relation to the presumed speed of language change (**Blackmore**; **Greenfield & Gillespie-Lynch**; **Pagel & Atkinson**) and level of selectional pressure (**Behme**); while others suggest that the argument cannot go through more generally (**Barrett et al.**; **Blackmore**; **Fitch**; **Hurford**), or that our arguments can be expanded to argue even against the possibility of the co-evolution of functionally relevant linguistic regularities (**Smith et al.**).

In the following sections, we discuss these themes in turn, and close by outlining open questions and challenges for future research that are raised by the commentaries. We conclude that the balance of the discussion suggests that a new synthesis concerning the relationship between brains, genes, and language may be emerging.

R2. Rethinking classical UG

The centerpiece of our argument was that there is no credible evolutionary account for a genetically based UG, throwing the classical conception of UG into difficulties. Many commentators are, largely on independent grounds, happy to accept that UG, as classically conceived, is not viable. For example, **Goldberg** argues that the traditional conception of UG should be replaced by an attempt to specify the cognitive and neural prerequisites for language, noting that recent advances in, among other things, the computational and psychological study of learning, require revisiting arguments for UG. Indeed, Goldberg and several other commentators (e.g., **Hurford**; **Wallentin & Frith**) note that Chomsky's own position can be read as rethinking the classical UG viewpoint. Thus, Hauser et al. (2002) have, as Goldberg notes, emphasized the importance of domain-general mechanisms, raising the possibility that recursion might be the only element of the "narrow faculty of language" – that is, a genetically based process, which is specific to language.

We agree with these commentators that, taken at face value, this theoretical position does seem to require letting go of core theoretical claims previously associated with UG. This move has substantial theoretical implications: It signals the need for a complete revision of the perspective that the goal of linguistics is the characterization of UG; a withdrawal of the claim that linguistics is a branch of biology; and a departure from viewing language acquisition as the "growth" of a language organ, whose blueprint is specified by the genetic constraints that encode UG. It seems, then, that Hauser et al.'s (2002) position is strongly in tension with those contemporary theorists who are committed to the view that language acquisition must be explained in terms of innate language-specific constraints, both in meta-theoretic discussions in linguistics (**Harnad**; **Reuland**; see also, e.g., Boeckx 2006) and accounts of language acquisition (e.g., Crain & Pietroski 2006).

Even if the conventional UG picture is set aside, some commentators suggest that there is, nonetheless, a role for language-specific innate constraints of some kind, especially in explaining how children can learn the enormously subtle and intricate patterns in natural language. Thus, **Satterfield** raises the point that a naive empiricist perspective on language acquisition might be expected to mirror the adult linguistic environment. But how, then, are systematic errors in children's speech to be explained? For example, how, she asks, is it possible to explain that children brought up in English-speaking linguistic environments frequently drop subject pronouns in tensed clauses (Hyams 1986), even though this is not observed in their linguistic environment? Satterfield suggests that we must look to innate language-specific biases to explain how this can occur. We agree with Satterfield that biases may be needed to explain this and other acquisition phenomena. However, whether such biases are specific to language is, of course, an empirical question. Indeed, recent analyses of children's spontaneous productions and computational modeling by Freudenthal et al. (2007) suggest that the omission of subject pronouns in English may be explained without recourse to language-specific information, by a simple developmental model incorporating cognitive processing constraints and which gradually acquires grammatical knowledge from distributional information in child-directed speech.

Also focusing on the role of innate constraints, **Reuland** provides a shortlist of requirements for an innately specified language acquisition system, going beyond the minimal conception of UG as containing only recursion (Hauser et al. 2002). These constraints appear highly language-specific in nature, such as a checking operation to compare linguistic features and a locality condition to restrict movement, depending on linguistic domains. Moreover, even if, in line with the Minimalist Program, much of the prior work of classical UG is pushed into a parameterized lexicon, non-lexical parameters are still needed in current versions of minimalist theory (Baker 2001; Boeckx 2006). Thus, despite the arguments put forward by Hauser et al. (2002), current generative accounts of language in linguistics appear to require UG to encompass considerably more abstract, language-specific properties than just recursion (at least given the current state of the Minimalist Program). As a consequence, such accounts are therefore vulnerable to the logical problem of language evolution described in the target article.

One potential way of rethinking UG is to reconceptualize it in more functional terms, which are outside the immediate scope of the arguments in the target article. **Satterfield** suggests that UG be construed as a collection of domain-general mechanisms that interact with language-specific components to help resolve the purported POS problem (see also Bever, in press). However, this perspective cannot escape the logical problem of language evolution, because of the arbitrary (i.e., nonfunctional) nature of the latter, language-specific, part of this hybrid UG. **Barrett et al.** push the reconceptualization of UG still further, proposing to conceive it simply as whatever mechanisms have evolved specifically for language – even if these should turn out to be entirely functional in nature and thus diametrically opposed to the claims of classical UG. As noted in the target article, we agree that evolution may have led to adaptations for certain functional features of language – though, as discussed further below, the extent of this is not clear (**Smith et al.**).

In contrast to these adaptationist reconceptualizations of UG, **Harnad** endorses our analyses of the problems facing adaptationist explanations of UG and instead backs a non-adaptationist account. However, as mentioned above and in the target article, this type of explanation faces a difficult dilemma. On the one hand, if UG is really so simple that it can come about through "chance" (e.g., via a single mutation), then it is not clear how it can resolve the purported POS problem, or other acquisition phenomena (as, e.g., highlighted by **Satterfield**), which are typically viewed as requiring rich language-specific innate constraints. On the other hand, if UG is permitted to have the complexity necessary to deal adequately with such acquisition issues (as hypothesized by many generative approaches), then the probability of such an intricate biological structure emerging de novo through a single macro-mutation is vanishingly small.

Also advocating a non-adaptationist perspective, **Piattelli-Palmarini et al.** suggest that we have underplayed the impact of the "evo-devo" revolution in biology for understanding how UG might have evolved by non-adaptationist means. The evo-devo approach has shown that biological evolution frequently exhibits the repetition and variation of basic "modular" structures, typically underpinned by common genetic machinery (Kirschner & Gerhart 2005).

Could this be true for UG? Chomsky (e.g., 1980) repeatedly stressed how the structure of language differs fundamentally from that observed in other cognitive domains. If this is right, it is very difficult to see how a unique, complex, and fully functioning system might spring into being as a minor variation of some existing cognitive structure. Similarly, if, as Piattelli-Palmarini et al.'s title appears to suggest, the design of language arises from optimality constraints, which might perhaps, as Chomsky (2005b) has recently suggested, be analogous to the minimum principles that give rise to soap bubbles and snowflakes, then it is unclear why special-purpose biological machinery for UG is theoretically necessary at all. In the target article, we therefore argued that the emergence by non-adaptationist means of a complex, functioning neural *system* embodying UG is astronomically unlikely. Indeed, as we read the literature, biological structures built de novo appear invariably to be shaped by long periods of adaptation (Finlay 2007). Thus, while antennae may be a modification of the insect leg (Carroll 2005), it is *not* an insect leg, or anything like one. It is exquisitely crafted to play its new role – and such apparent design is universally explained within biology as an outcome of Darwinian selection. The impact of evo-devo is to help us understand the intricate structure and constraints of the space of organisms over which the processes of variation and natural selection unfold; it is not an *alternative* to the operation of natural selection (Carroll 2001).

R3. Too much emphasis on the brain?

The title of our target article, "Language as shaped by the brain," embodies the claim that the brain, and the thought-based, perceptuo-motor, cognitive, and socio-pragmatic processes that it supports, plays a crucial role in determining the structure of natural language. Yet, as we pointed out, the influence of these processes can take a wide range of routes. Many of our commentators explore the possibility that our emphasis on the brain may be excessive (**Catania**); or that it should at minimum be supplemented with an analysis of the selective forces on language generated by its communicative function, and its transmission across networks of individuals (**Brooks & Ragir**; **Smith et al.**; **Wallentin & Frith**). According to this latter viewpoint, there may be regularities in language that can be understood independently from the details of brain mechanisms. In general, a natural challenge to our perspective on the evolution of language structure is to ask, from an explanatory point of view: How much can be explained by cultural transmission alone?

Catania suspects that, in using the brain to explain linguistic behavior, we have the cart squarely before the horse. Instead, he sees behavior as primary and argues that human learning mechanisms may be flexible enough to capture and reflect whatever patterns of behavior may be required. He uses the analogy of categorical perception (Liberman et al. 1957). While many theorists suggest that categorical perception between phoneme boundaries may arise from boundaries in the sensory input or the mechanisms of speech perception and/or production, Catania contends that it may be more productive to propose that such boundaries are not so constrained. Instead, the specific boundaries observed in categorical perception in different languages may be determined purely by the linguistic environment (i.e., English vs. Arabic) – according to this viewpoint, the brain is not shaping language, but responding to the linguistic environment.

We suggest that this viewpoint is not adequate to explain linguistic regularities in general, however, precisely because it does *not* place constraints on the patterns of language that are viable. The challenge of understanding language structure is to explain the structural regularities that the world's languages do, and do not, exhibit; and some of the key sources of constraints are, we suggest, that languages must be easy to learn (from limited amounts of data that are available to the child), that they must be easy to process (e.g., linguistic relations will typically be local, rather than involving arbitrarily long and complex dependences between linguistic items), and that they must fit naturally with the perceptual and motor apparatus (language must be easy to decode, and easy to produce).

A lack of focus on such constraints is, we suggest, also evident in many meme-based accounts of cultural and linguistic evolution, as exemplified in the commentary by **Blackmore**. She suggests that language should be viewed as a complex of memes; and that these memes propagate in a *selfish* way – that is, the crucial factor in language evolution is the replicative power of memes, independent of any functional value that the memes may or may not have for their "hosts," that is, language users. We are wary of this perspective if taken to an extreme. We would agree that understanding which aspects of language structure will readily be transferred from one generation of language users to another is critical in understanding the selectional pressures on languages. But we see the question of the learning and processing biases of learners to be crucial in determining what is, or is not, readily transferred. That is, which structures "replicate" depends critically on the nature of the brains that propagate those structures via learning. Thus, we see the selection pressures on language as arising, to a large degree, from the properties of the brain.

Piattelli-Palmarini et al. appear to have mistaken our approach for a meme-based account (such as **Blackmore's**) and are concerned that viewing language as a cultural product means that linguistic evolution is no different, in principle, from the design of a Boeing 707. But, of course, aircraft are typically products of directed and determined efforts of design, typically by vast teams of scientists and engineers. The process of the cultural construction of language is, we suggest, a much more piecemeal, distributed, and incidental matter. In specific circumstances, with particular purposes in mind, people attempt to communicate; and the layering of such attempts, and their selective winnowing and replication, inadvertently creates a language, shaped by the brain. The putatively worrying analogy with aircraft design therefore seems remote at best.

More generally, a tendency to see processes of cultural transmission as an *alternative to*, rather than as *grounded in*, theories of brain and cognition occurs elsewhere in the literature. For example, many properties of language are viewed as arising from historical processes of language change (such as grammaticalization); and such processes are viewed as fairly independent of underlying brain mechanisms (Bybee, in press). But we argue that processes of historical language change depend crucially on the cognitive and neural machinery of the speakers involved. Even if language

is a cultural product, created by processes of cultural transmission, it is nonetheless shaped by the brains that create and transmit linguistic structure. The brain, and the cognitive and learning constraints that it embodies, is centrally important, after all. **Brooks & Ragir** generalize this line of thought to cultural products more broadly, suggesting that tool manufacture, music, and play are all likely to be shaped by an interplay of factors governing cultural transmission and the cognitive constraints of individual agents. We shall discuss later on how far the arguments of our target article, particularly concerning the non-viability of nativism with respect to apparent universals, might apply beyond language to other aspects of culture.

One way to study the interplay of constraints on learners and the structure of the cultural transmission of language is through the combination of computer simulations – where both the "cognitive machinery" of the learners and the structure of communicative interactions, including the structure of the "social network" across which information is diffused, can be directly manipulated. **Smith et al.** mention their important work in this tradition, which we shall discuss in detail later. A complementary approach is to study the diffusion of information across human agents, as outlined by **Caldwell**. She finds intriguing cases of "convergent evolution" in problem-solving tasks, when solutions are passed from "generation to generation" by gradual replacements of group members. Here, the selectional pressure (the preference for one solution over others) results from explicit reflection and discussion within the group, rather than the presumably nonconscious biases that shape many aspects of language evolution. Nonetheless, this work provides an intriguing illustration of how the properties of learners (here, their problem-solving abilities and biases) can lead to systematic regularities, which may converge across groups. Perhaps similarly, convergent evolution at the level of language change might explain some common properties across the world's languages. Thus, the interplay of computer simulations and empirical research promises to be particularly fruitful for the investigation of such convergent evolution.

R4. The biological and cognitive basis of language

In the previous section (R3), we considered commentaries that emphasize the importance of learning, communication, and properties of cultural transmission – but we have stressed that these processes are grounded in the properties of our cognitive and neural mechanisms. Here, we consider commentaries for which those mechanisms are the main focus. That is, we consider questions such as: What are the cognitive pre-adaptations that make the cultural construction of language possible? What is distinctive about human cognition? And, more broadly, how is language rooted in biology?

Before addressing these questions, it is important to distinguish the main points at issue, which concern the general biological machinery that makes language possible (which, it is typically assumed, is shared by all normally developing humans), from the question of individual variation in linguistic ability. **Pagel & Atkinson** rightly point out that human linguistic abilities, like most human cognitive differences, are quite strongly heritable, implying that these differences have a genetic basis. Such differences need not, of course, be language-specific, but might reflect general processing differences, such as variations in memory (**Landauer**; see also, e.g., Ericsson & Kintsch 1995; MacDonald & Christiansen 2002; Wynne & Coolidge 2008). Moreover, "generalist" genes may explain a broad range of learning abilities and disabilities (Kovas et al. 2007). In the target article, however, the focus is not on genes that vary between language users, but on the common genetic basis, shared across the normally developing population, that supports language acquisition and processing. The range of suggestions concerning the key biological and cognitive bases for language mentioned in the commentaries is impressively broad.

De Ruiter & Levinson argue that the key driving force behind language is *communicative intelligence*: a powerful pragmatic system for relating signals to communicative intentions. They argue that this system arose prior to language, and that this adaptation crucially distinguishes the human brain from that of other primates (for a related perspective, see Tomasello 2008). This approach provides an elegant inversion of the assumptions common in nativist perspectives on language acquisition. According to that tradition, the distinctive features of the language organ concern the abstract, structural properties of syntax and phonology; pragmatic inference is typically assumed to be continuous with general inference abilities (e.g., Fodor 1983), and hence not properly part of the language system at all, let alone part of UG. Yet, de Ruiter & Levinson take pragmatics to be the cognitively decisive mechanism for the emergence of language; and Levinson (2000) suggests, as we briefly described in the target article, that highly specific and intricate structural patterns in language, such as the binding constraints, emerge as a consequence. This concrete example of how general communicative factors can generate apparently highly arbitrary and complex syntactic phenomena illustrates the potential value of viewing language as adapted to the brain, rather than the reverse. This case is perhaps particularly interesting, given that binding constraints are often highlighted as particularly strong evidence for innate linguistic constraints (**Reuland**).

Enfield makes a related argument, focusing instead on the primacy of the speech act, a pragmatic notion concerning the unit over which communicative intentions are conveyed. He argues that the structure of communication as a series of conversational "moves and countermoves" may have strong implications for the structure of grammar. **Fauconnier & Turner**, by contrast, argue that human evolution may have undergone a qualitative and decisive *cognitive* transition involving the ability to engage in "double-scope blending." This ability permits the integration of two different representational frames, which Fauconnier & Turner take to underlie the creation of not merely language but many aspects of culture, from mathematics to religion. We suggest that the complexity and variety of cognitive machinery that presumably underlies the full range of cultural products, including language, makes the existence of a single key transition prima facie unlikely; but this bold possibility is certainly worthy of consideration in principle.

Tallerman takes up a complementary line of reasoning, in considering cross-linguistic regularities in case-marking systems. She notes that case-marking tends to be highly "economical" – that is, while a variety of possible linguistic cues

may be used to signal case, cues are used only where necessary to avoid ambiguity. Typically, overt case-marking only applies to one member of an "opposition" (e.g., between agent and patient); the identity of the non-marked case may, presumably, be "filled in" by the listener using the type of pragmatic inferences considered by **de Ruiter & Levinson**. Tallerman's account explains some of the variety of case systems observed cross-linguistically, from a purely functional standpoint (e.g., in terms of economy and avoiding ambiguity). Her arguments thus provide a counterweight to **Satterfield**'s claim that innate knowledge of case systems may have to be built into the learner. Clearly, children are able to acquire case systems for natural language – but this may be explained because case systems have evolved to be functionally effective, and, we suggest along with Tallerman, readily learned and processed. Thus, case systems, along with other linguistic regularities, will reflect whatever learning and processing biases the cognitive system embodies. But this match arises not because the learner has a language-specific innate knowledge of the case system, but instead because the case system has been selected to fit language learners and users.

Wallentin & Frith take a different tack, developing an intriguing argument. They first point out that perceptuomotor constraints are likely to be important in constraining language, noting that imaging studies suggest that neural representations of different classes of words are located in corresponding brain areas (e.g., action words are often associated with prefrontal cortex [Hauk et al. 2004], whereas words representing spatial relations are associated with posterior parietal cortex [Wallentin et al. 2006]). Nonetheless, they note that, in many areas of classification (e.g., color names), there is considerable variation across languages, even though color names appear to be driven, to some extent at least, by considerations of perceptual optimality (Regier et al. 2007). Wallentin & Frith suggest that this may arise because the drive to align with other group members may outweigh the drive to find an optimal classification. They suggest that the goodness of a classification may partially be defined in terms of agreement with other group members, which may potentially lead to a radical and rapid runaway process. We suggest that such processes may be particularly likely where there is a large range of alternative solutions, which are roughly equally "good" from the point of view of the individual agent; and especially when it is difficult to shift from one type of solution to another. Many of the arbitrary aspects of the world's languages, ranging from the inventory of phonemes, the variety of syntactic categories, to the functioning of pronouns, seem to exhibit considerable variation. These variants are, perhaps, roughly equally good solutions; and moving between solutions is slow and difficult (although historical linguistics does sometimes indicate that change does occur between such forms; McMahon 1994). In such cases, the selection pressure on language from the brain imposes only a relatively weak constraint on the solution that is reached. Conversely, the functional pressure for the emergence of other aspects of language, such as double articulation (i.e., separate combinatorial layers of phonological and syntactic structure) or large vocabulary (**Hurford**) or compositionality (**Smith et al.**), may be so strong that these factors are not disturbed by social forces.

Greenfield & Gillespie-Lynch also consider perceptual-motor factors to be an important, but insufficient, starting point for understanding language. They argue that the structure of actions may provide an infrastructure for linguistic behavior (see, e.g., Byrne & Byrne [1993] on the complex action sequences involved in field observations of gorilla leaf-gathering). This infrastructure might be co-opted in gestural communication. Yet, like **Wallentin & Frith**, Greenfield & Gillespie-Lynch argue that social factors are likely to play a key additional role. They suggest that mirror neurons, which are phylogenetically broad, may be indicative of "intersubjectivity" (i.e., the sharing of mental states by two or more people), and that this may be crucial to language (as is indicated by, for example, work on joint attention in developmental psychology; Eilan et al. 2005). Mirror neurons appear to represent actions, whether performed by the agent or merely observed; and, suggestively, mirror neurons are located in what is arguably the homologue of Broca's area, which is important for language in humans. Differential expansion of language-related areas in the human brain may, Greenfield & Gillespie-Lynch suggest, indicate co-evolution of brain and language.

We suspect that such arguments may currently be premature. Although a number of experiments have been conducted to investigate mirror neurons in humans, the results remain unclear (for discussion, see Turella et al. in press). Another caveat is that mirror neurons were originally found in a nonhuman primate, and may even be present across a wide range of species (Hurford 2004), indicating that mirror neurons may not be a key factor in language evolution. Moreover, there are elegant statistical models that accurately show the relationship between the differential expansion of brain areas across a wide range of mammals. These models reveal no notable expansion of Broca's or Wernicke's area, as might be expected from selectional pressure for language (Finlay et al. 2001). Although these considerations caution against the specific scenario for language evolution outlined by **Greenfield & Gillespie-Lynch**, the argument of our target article does not deny the possibility of brain-language co-evolution. Rather, the logical problem of language evolution arises for *arbitrary* properties of language – because, having no "functional" anchors, these will tend to vary freely and rapidly, both across time and across populations. This would lead to a highly unstable linguistic environment, to which slow-changing language genes cannot readily adapt. But this specific argument does not eliminate all possibility of co-evolution between genes and behavior. For example, it is entirely compatible with our argument that better memory (**Landauer**) or better pragmatic skills (**de Ruiter & Levinson**; **Enfield**; **Wallentin & Frith**), might co-evolve with a language system that draws upon these skills. We shall discuss these issues in more detail, as they arise throughout the commentaries, in section R5.

Lieberman has a different proposal concerning the key neural circuitry underpinning language and a range of other human-specific behaviors, such as dance and music. He focuses on neural circuits creating bidirectional links between the cortex and basal ganglia. As also noted in the target article, the corticostriatal system is important for the learning and processing of sequential information (Packard & Knowlton 2002). Lieberman further argues that "hard" data from molecular genetics and neuroimaging suggest that these neural circuits underpin our productive syntactic capacity. For example, mutations in the FOXP2 gene, which has been shown to be crucial to the

development and function of the corticostriatal system (Lai et al. 2003), give rise to severe speech and orofacial motor problems (Lai et al. 2001; MacDermot et al. 2005). This genetic link between sequential learning and language is further underscored by recent results showing that common allelic variation in FOXP2 is associated with individual differences in performance on a sequence-learning task, which, in turn, is related to language ability (Tomblin et al. 2007). Thus, genetic research relating to brain development can readily be incorporated into the new synthesis proposed here, providing insights into the nature of the neural constraints that shape language evolution.

Emphasizing the importance of constraints arising from the human body, **Aronoff et al.** and **Corballis** explore the contribution of gesture to language evolution. Indeed, Corballis sees gesture as the origin of language, arguing that early languages may have been signed, rather than spoken. He argues that the scenario for language evolution outlined in the target article is compatible with a gestural origin of language. We see this as an important possibility. It is certainly conceivable that early language – as a cultural product – might equally well have been shaped by the mechanisms involved in the production and interpretation of gestures as those used for vocalizations. Research on modern apes suggests that vocal and manual gestures might initially have proceeded in parallel, perhaps with a more flexible use of gestures (Pollick & de Waal 2007). Subsequent changes to the human vocal tract might then have tipped the scales toward speech as the default modality for language (irrespective of whether these anatomical changes were adaptations specifically for speech [Lieberman 1984] or something else [Hauser & Fitch 2003]). We remain agnostic with regard to these questions of language origin, but we note that – perceptuo-motor differences notwithstanding – there is considerable overlap in mechanisms between spoken and signed languages that would allow for much similarity in the thought-based, cognitive, and pragmatic constraints imposed on their evolution (as outlined in the target article).[2]

Further highlighting the importance of gesture, **Aronoff et al.** point to newly emerging sign languages as a source of evidence of language evolution in vivo. Specifically, they argue that a key discontinuity between humans and other primates is *iconicity*: While nonhuman primates in the wild spontaneously gesture, they appear never to use gesture to represent external objects or events. It is interesting to ask how this difference may relate to cognitive distinctions discussed by other commentators, including **de Ruiter & Levinson**'s communicative intelligence. Perhaps the key to being able to interpret a gesture as a representation is understanding that the gesture is a signal that is intended to convey a message; and producing a gesture as a representation requires understanding that the other agent will understand this intention; and so on. A complementary suggestion is **Corballiss**' proposal that "mental time travel" – the ability to mentally replay past events, or imagine future events – may underpin symbolic representation, which allows reference to items that are not perceptually present.

While **Aronoff et al.** see iconicity as a starting point for (signed) language, **Dessalles** views it as a crucial limitation. He argues that if language has been shaped by the brain, then we should expect that iconicity should be maximized, because this would make learning as easy as possible. Yet, as de Saussure (1916/1959) observed, relations between linguistic signs and their meanings are typically close to arbitrary. We believe this concern can be readily allayed by noticing that language is selected not just to be learnable, but also to be communicatively effective (that is, forms which do not successfully convey their message will be eliminated). As **Namy & Nygaard** point out, *communicative* pressures favor arbitrariness. An iconic representational system will preserve the similarity relations of the represented domain in the signs themselves. Although communication often requires distinguishing between signs for closely related things, context typically can tell us what a sign is referring to (e.g., a species of fish, a brand of car, or a TV show). An iconic system of representation will be communicatively inefficient if the signs for each type of object are highly similar, and hence contextually redundant and difficult to distinguish, both in production and perception. Developing this idea, Monaghan and Christiansen (2006) illustrate the advantages of an arbitrary, rather than a systematic, phonology-semantics mapping, in simulations with a feed-forward connectionist network. Nonetheless, the model also indicates that systematic mappings may arise in the service of learning about other aspects of language (e.g., in the form of phonological cues to lexical category; Monaghan et al. 2007). As noted by Namy & Nygaard, this illustrates the idea of language as adapting to multiple competing constraints.

Stressing the importance of communication, as well as learning, in shaping the evolution of language also resolves another of **Dessalles**'s concerns. He suggests that if languages are selected to be learnable, then linguistic complexity will gradually be stripped away, leading ultimately to a "null" language. But such a language will not evolve, precisely because it would have no expressive power, and hence would be communicatively useless. The complexity and diversity of language arise because the primary purpose of language is rich and flexible communication.

Goldberg raises a more subtle version of the same issue. Should we expect that, through successive generations, languages will become increasingly easy to learn? Might this imply, perhaps implausibly, that Creoles would be especially difficult to learn? Goldberg notes, though, that such predictions do not immediately follow, precisely because language has to simultaneously satisfy constraints concerning expressive power, and ease of learning and processing. The drive for expressive power will typically lead to greater complexity, balanced by a drive for ease of learning and processing, which pushes toward greater simplicity. Note that the constraints from learning and processing may also be in opposition – and some aspects of language change may crucially arise from this opposition. For example, historical language change involves both processes of erosion (i.e., reducing morphemes, creating irregular forms, and thus reducing the load on language production) and regularization (making learning easier) (McMahon 1994).

But how much of language change is due to child language acquisition (Bickerton 1984), or is linguistic variation primarily created and propagated through adult populations (e.g., Bybee, in press)? To the extent that child language acquisition is the major driver of change, the processes of cognitive development are likely to be important in understanding language change (**Toscano et al.**). We are sympathetic to this general perspective (cf. Karmiloff-Smith 1992), although the current state of

understanding of the learning and processing mechanisms across development may currently be insufficient to constrain closely the theory of language evolution. **Brooks & Ragir** also stress the importance of development – and in particular the prolonged neural plasticity that seems especially characteristic of humans. We see prolonged development as a consequence of the need to construct highly complex, yet flexible, cognitive functions. Indeed, to the degree that cognitive development must be responsive to the particular culture (including the particular language) to which the child must adapt, a prolonged period of learning from the environment (whether physical, social, or linguistic) is surely necessary.

Brooks & Ragir argue that our target article is insufficiently radical, however. They wish to go beyond our claim that language does not presuppose a genetically specified UG, to argue against the existence of genetically encoded cognitive pre-adaptations for language. To the extent that a pre-adaptation for language is a mechanism or process that has adapted through natural selection, but not to support language, the claim that such pre-adaptations exist seems relatively mild. Indeed, the various claims concerning cognitive and biological prerequisites for language reviewed above all seem plausibly to fall into the category of pre-adaptations. Yet we suspect that Brooks & Ragir's aim is not to deny the existence of pre-adaptations. Rather, it is to deny that the development of any specific pre-adaptation was the trigger for the creation and evolution of language. Instead, they suggest that changes in habitat, diet, and social organization might be more important. To the degree that language is viewed as a cultural phenomenon, this perspective seems plausible. Scholars do not seek to identify a crucial biological change in the hominid lineage supporting the development of agriculture, fire, or arithmetic – it may be that this is equally futile in the case of language. Nonetheless, language does appear to be uniquely human. Even if there is no single critical difference between humans and other animals, it still seems to be an important scientific project to sketch out the dimensions on which humans are biologically and cognitively special.

More broadly, the commentators on this target article have provided a rich set of hypotheses that deserve further exploration, illustrating the potential pay-off that may be obtained by attempting to understand language as shaped by the brain, and thereby countering **Piattelli-Palmarini et al.'s** concern that our approach has no explanatory bite.

R5. When can genes and language co-evolve?

Our target article makes a narrowly focused argument against the hypothesis that genes *for arbitrary features of language* (as in UG) could have co-evolved with the language itself. In a nutshell, the concern is that, lacking any functional pressure to stabilize them, and prior to the existence of putative language genes, such arbitrary features of the language will vary. Indeed, we suggest that language change is typically very much faster than genetic change, and, hence, that the linguistic environment will provide a moving target, against which biological adaptation will not be possible. We noted also that the spatial diffusion of human populations would be expected to lead to a wide diversity of languages (and, indeed, human languages appear to diverge very rapidly – Papua New Guinea was probably settled less than 50,000 years ago, and yet it contains perhaps one quarter of the world's languages, exhibiting an extraordinary diversity in phonology and syntax; Diamond 1992). Co-evolutionary processes can, of course, only adapt to the current linguistic environment – and hence the variety of languages would, through co-evolution, generate different selective pressures on "language genes." Yet modern human populations do not seem to be selectively adapted to learn languages from their own language groups – instead, every human appears, to a first approximation, equally ready to learn any of the world's languages (but see Dediu & Ladd 2007).

Although the target article is clear about the narrow scope of this argument, and, indeed, explicitly notes that it does not necessarily apply to functional aspects of language, several commentators take our argument to be rather broader: to amount to the claim that no aspect of cognition can be positively selected for language, or even that co-evolution between any pair of processes is not possible. In the light of this misreading of our argument, several points of concern from the commentators can be set aside.

In particular, **Blackmore** raises the concern that possible (although controversial, see Hauser & Fitch 2003) evidence that the larynx has been adapted to improve speech articulation would cast doubt on the viability of our argument against the co-evolution of language and language genes. Note, though, that improvements in the speech apparatus would have a positive and general functional impact on language behavior, whereas genes for UG are expressly for arbitrary features of language – and it is the latter that is the subject of our argument. **Barrett et al.**, similarly, develop an argument that language-gene co-evolution is possible, in principle. We entirely agree (see Christiansen et al. 2006, for simulations of the biological adaptation for functional features of language). Our arguments apply only to the viability of co-evolution of genes for arbitrary features of language, and Barrett et al.'s counterarguments do not address this.

Fitch puts forward what appears to be a more direct attack on our position: "If this 'logical problem of language evolution' is indeed as severe as C&C claim, it is not just linguists who should be worried: any biologist interested in adaptation to a rapidly changing environment (e.g., individual learning) or culturally transmitted system (e.g., bird or whale song) should be alarmed." The first case does not seem directly relevant. Fitch notes that adaptation to a rapidly changing environment typically leads to "generalist" species (e.g., rats) whose behavior is highly responsive to the environment; the natural parallel would be to assume that language learners would be generalists, able to deal with a broad range of linguistic environments. But, before the putative UG is established, early languages will not exhibit any specific set of arbitrary constraints – and hence, to deal with this range of languages, the generalists will not embody such constraints either. So this line of reasoning seems to lead directly to the conclusion for which we are arguing.

The case of learned bird- and whalesong appears more directly analogous to language (see also **Pagel & Atkinson**). **Fitch** points out that biologists agree that the songs of some species of birds are culturally transmitted, but within sharply defined limits. Moreover, he notes, biologists agree that birds have an innate propensity ("instinct") to acquire the song type specific to their species (Marler 1991). This seems analogous to the case of human language: Language

is culturally transmitted, and people may have an inherent disposition to acquire human languages. Fitch may perhaps suspect that we do not accept that people have any such innate propensity for language – but, in the weak sense of the term "relevant" here, our position entails that there is indeed a genetic basis for language, in the form of a range of pre-adaptations (perceptuo-motor, communicative, cognitive, and so on). We deny, though, that there is a genetically encoded language-specific UG; and we explain the viability of acquisition, and the structure of the world's languages, in the light of the adaptation *of language* to this genetic basis. **Goldberg**'s quote from Liz Bates puts the point well: "It's not a question of Nature vs. Nurture; the question is about the Nature of Nature" (Bates 1993).

Fitch goes on to develop an argument that comes dangerously close to undercutting his position. He agrees that rapid cultural changes imply that genetic changes (whether in the bird or human case) will only be positively selected for properties that are stable across that cultural environment – this is the "generalist" strategy, mentioned earlier. But *prior to the existence of language-specific genetic constraints*, arbitrary properties of language, such as those in a putative UG, will precisely not be stable: they have (by assumption) as yet no genetic basis; and (also by their presumed arbitrariness) they have no functional role to ensure they dominate the cultural environment. Hence, the arbitrary constraints of UG will be just the kinds of features that will not be genetically internalized.

Barrett et al. also observe, rightly, that co-evolution between language and genes is possible, noting that even a fast-changing environment will have statistical properties which may, to some degree, provide selectional pressure on learners. As they point out, co-evolution appears widespread in biology (e.g., Futuyma & Slatkin 1983). There are, moreover, some well-attested cases of co-evolution between culture and genes. For example, the development of arable agriculture and dairying appear to have co-evolved with genes for the digestion of starch (Perry et al. 2007) and lactose (Holden & Mace 1997). Note that these cases are examples of stable shifts in the cultural environment – for instance, once milk becomes a stable part of the diet, there is a consistent positive selection pressure in favor of genes that allow for the digestion of lactose. These cases are entirely consistent with our position: Co-evolution can and does occur where culture provides a stable target. But this could not be the case for the putative arbitrary regularities presumed to be encoded in UG. We concur with Barrett et al. that the broader project of understanding what cognitive mechanisms may have been positively selected for because of their role in language acquisition and use (e.g., **de Ruiter & Levinson**'s communicative intelligence; increased memory capacity allowing a large vocabulary [**Landauer**]; or the structure of the vocal apparatus, mentioned by **Blackmore**, and so on) is an important direction for future work.

Several commentators note that our arguments rest on the assumption that language changes more rapidly than genes and that this assumption is open to question (**Behme**; **Blackmore**). **Pagel & Atkinson** report some important recent analyses which suggest that some aspects of language may change surprisingly slowly. The Indo-European language group shows common aspects of vocabulary over many thousands of years, as shown both by traditional linguistic analysis and modern statistical methods (Pagel et al. 2007). Nonetheless, these languages have gone through spectacular divergences and reorganizations, which scarcely count as a stable linguistic environment over either time or space. Moreover, while, as Pagel & Atkinson point out, the lactose gene may have become established over a period of thousands of years, it is unlikely that a single gene would be responsible for establishing an arbitrary linguistic regularity, such as some aspect of the binding constraints. This would suggest that an even longer period of stability in the target language would be required for the relevant genes to become established. Overall, we suggest that our assumption that languages change faster than genes is a good first-order approximation – and this creates substantial difficulties for co-evolutionary accounts of the origin of UG. Nonetheless, Pagel & Atkinson's arguments raise the possibility that this assumption is not always correct, and suggest that further analysis may be required to see if there are limited circumstances where language-specific arbitrary constraints might become established.

A number of commentators point to specific evolutionary mechanisms that, they suggest, might extend or complicate our argument somewhat. **Behme** notes that our argument may be strengthened by the observation that language users need to coordinate with each other – a dramatic grammatical "advance" for a single agent might not confer selectional advantage. It would, one might say, be comparable to being the only person to own a telephone, which is useless unless there is someone with whom to communicate.

Behme further suggests that powerful forces of sexual selection may change the argument in favor of biological adaptations for language by analogy with the male peacock's impressive tail feathers (see also **Dessalles**). Indeed, the males of many species of songbirds use their vocal prowess to attract females and defend their territory, and have clearly been subject to sexual selection (e.g., Catchpole & Slater 1995). Crucially, however, such sexual selection has resulted in considerable sexual dimorphisms in the neural systems for song, with males having substantially larger brain areas for song control (e.g., MacDougall-Shackleton & Ball 1999). Similarly, sexual selection for language ability in humans would also be expected to lead to sexual dimorphisms in the brain areas involved in language, but there is no evidence for such neural differences favoring male linguistic ability. If anything, human females tend to acquire language earlier than males (e.g., Dionne et al. 2003) and to become more proficient language users (e.g., Lynn 1992). Thus, it would seem that sexual selection is unlikely to be a major determinant of any biological adaptations for language.

Hurford argues that the mechanism of "Baldwinian niche construction" may provide a route for the co-evolution of genes for some, albeit limited, language-specific knowledge or mechanisms. Perhaps some change in the structure of hominid social groups (e.g., group size) may have changed the "niche" in which communication occurs; and this might itself have altered the dynamics of language change and the selectional pressures on cognitive machinery co-opted for language processing. If this is right, then the triggers for the initial creation of language may have been social, rather than biological, change (as **Brooks & Ragir** also argue). Hurford suggests, in line with our target article, that it is possible that *functional* (rather than arbitrary) features of language might subsequently co-evolve with language, and he highlights large vocabulary, double articulation, and

long-distance dependencies as possible language-specific structures. We welcome these specific proposals, and see them as valuable pointers to guide future empirical work.

Smith et al. suggest that our argument that arbitrary aspects of language cannot become genetically fixed by co-evolution applies equally well to functional aspects of language. They cite important recent formal analyses by Kirby et al. (2007), which indicate that, if learners choose the most probable language, given the linguistic data to which they have been exposed, then the *ordering*, but not the *strength*, of their prior biases, determines the distribution of languages that arise from cultural transmission. Smith et al. raise the concern that, in this type of case, there may be no pressure of natural selection on the more "desirable" priors – and hence that genes that influence such priors may be "shielded" from processes of natural selection. We suggest that this conclusion need not follow, however. The space of possible grammars (or, more broadly, hypotheses concerning linguistic structures) is vast; and hence the number of possible orderings of prior probabilities across this space is enormous. If genes influence this ordering, rather than the precise numerical values of the priors for each element in the ordering, this gives plenty of scope for enormous genetic influences on the speed of learning, and hence provides scope for strong selectional pressure on genes. Thus, *if* functional features of language provide stable constraints on the linguistic environment, then there could, we suggest, be strong pressures of natural selection on genes determining the ordering of priors over different grammars. Hence, we currently see in principle no reason to rule out the co-evolution of language and language genes for functional (though not arbitrary) constraints on language. Nonetheless, we suggest that additional experimental, computational, and theoretical work is required to clarify the circumstances under which such co-evolution is possible.

R6. Where next?

A decade ago, Lewontin (1998) painted a bleak picture of evolutionary accounts of language and cognition as being "nothing more than a mixture of pure speculation and inventive stories" (p. 111). In the target article, we outlined the beginnings of a new synthesis for theorizing about the relationship between brains, genes, and language, emphasizing the role of cultural evolution. This perspective views language evolution as primarily a matter of cultural, rather than biological, evolution; and such evolution is seen as continuous with processes of historical language change, such that selection among linguistic forms is driven by constraints concerning cognition, communication, learning and processing, and the structure of the perceptuo-motor system. These selectional pressures can be studied directly by analyzing the neural, cognitive, and social basis of language in modern humans, by exploring the impacts of different patterns of social transmission of linguistic patterns, and by analyzing contemporary and historical language change. The positive and constructive spirit of the commentaries gives us grounds for optimism that a synthesis drawing together these, and related, perspectives, is not merely attainable in principle, but is also likely to be of considerable scientific potential. Thus, the commentaries have highlighted a range of key areas for future work, and some important theoretical challenges. In this concluding section, we draw together these issues and identify central remaining open questions.

R6.1. Reconnecting synchronic and diachronic linguistics

We argued, in the target article, that grammaticalization and other processes of linguistic change are likely to provide much insight into language evolution. In a similar vein, we find that some of the key observations made by the commentators based on synchronic language data could be strengthened and emphasized by embedding them in a diachronic perspective. For example, **Tallerman**'s discussion of the typological patterns of case-marking as an example of linguistic adaptation could be further corroborated by incorporating diachronic data to explore the patterns of change over time, perhaps revealing more about the specific cognitive constraints involved. This point is underscored by **Aronoff et al.**, who describe how their study of in vivo changes in Al-Sayyid Bedouin Sign Language and Israeli Sign Language has highlighted the importance of body-based perceptuo-motor constraints on diachronic change. More generally, as noted in the target article, the combination of diachronic and synchronic analyses in past work has tended to show how apparently "arbitrary," language-specific linguistic universals might derive from general, cognitive constraints. The implication of this line of argumentation goes beyond theories of language evolution to the theory of language itself. For example, it seems that construction grammar may provide a much more suitable formal approach to capturing the properties of language than generative grammar in its various guises.

R6.2. Dynamics of linguistic and cultural change

Several commentators stress the importance of cultural dynamics in shaping language, some arguing that the social structures underpinning language transmissions from generation to generation may be as important as the cognitive and biological machinery of the language learner in determining the emergence and evolution of language. **Smith et al.** report computational models of language evolution, which illustrate the interdependence of assumptions about learners and mechanisms of transmission (Smith & Kirby 2008); **Caldwell** illustrates how cultural transmission can be studied in the laboratory. We suggest that there is much foundational theoretical work to be done in understanding the co-evolution of genes-for-learning and the structure of the to-be-learned domain, whether this domain is language or some other aspect of human culture. Only with such work in place will it be possible to assess the scope of the arguments presented here (e.g., whether functional aspects of language can become genetically embedded) and to determine how far our negative conclusions concerning UG might extend to putatively innate "grammars" in other cultural domains (e.g., morality; Hauser 2006). This work is required in order to extend existing theories of co-evolution (without learning or cultural change; Thompson 1994) and cultural evolution (without genetic change; Boyd & Richerson 2005).

R6.3. Relevance to language acquisition

The target article notes that language change, and consequently language evolution, may be importantly shaped

by language development, although language change in adults is also likely to be important (Bybee, in press). **Toscano et al.** and **Brooks & Ragir** elaborate on the importance of developmental processes embedded in a social context. Moreover, the target article noted that if language is shaped by the brain, the problem of language acquisition may be far less daunting than is typically assumed: Language has been shaped to be learnable from the noisy and partial input that children receive. Therefore, language will embody the (typically non-language-specific) biases or constraints the child brings to the problem of language acquisition. This dramatically reduces the impact of the POS argument, which is still used as a key motivation for UG (**Harnad**). These issues are explored in more detail in Chater and Christiansen (submitted).

R6.4. Revisiting the multiple constraints on language evolution and acquisition

The commentators elaborate and expand upon the four types of constraints (thought, perceptuo-motor, cognition, and social-pragmatic) on language evolution discussed in the target article, indicating that this framework is productive. Some highlight specific aspects of *thought* processes which may underpin language, such as mental time travel (**Corballis**) and double-scope blending (**Fauconnier & Turner**); some focus on *perceptuo-motor* constraints, including the importance of embodiment (**Aronoff et al.**) and the structure of actions (**Greenfield & Gillespie-Lynch**). **Lieberman** sees language as built upon a neural system for complex and flexible action sequences, underpinning the *cognitive* aspects of language processing and learning (**Namy & Nygaard**). Finally, several commentators stress the *social-pragmatic* forces that shape language, focusing on social interaction (**Wallentin & Frith**), communicative intelligence (**de Ruiter & Levinson**), and speech acts (**Enfield**). As noted in the target article, one of the major challenges for future research is to understand the many facets of each type of constraint, and how these constraints interact to shape the evolution of language.

R6.5. What makes humans special?

If the mechanisms shaping language evolution are to a large extent not specific to language, then what differentiates human cognition and communication from that of other primates? That is, why do humans have languages whereas other primates do not? Across the commentaries, there is a continuum of views, from the reiteration of the conventional viewpoint that grammatical information is innate and species-specific (**Harnad**; **Reuland**), across the suggestion that some such information may be a relatively small part of the story (**Barrett et al.**; **Satterfield**), to the idea that cultural and/or developmental processes are of central importance (**Brooks & Ragir**; **Smith et al.**; **Toscano et al.**). In considering human/primate differences, however, it is important to keep in mind that the absence of language-specific constraints on language does not necessarily entail the lack of species-specific constraints. Along these lines, **Hurford** and **Landauer** propose some specific cognitive features that may be uniquely human, including memory capacity sufficient to store a large vocabulary, double articulation, and combinatorial operations. Other commentators suggest that pragmatic machinery for interpreting others' behavior may be more fundamental (**de Ruiter & Levinson**). Comparative work on primate versus human neural and cognitive mechanisms, as well as archaeological analysis and language-reconstruction to clarify the relationship between biological changes and the emergence of language, will be crucial in addressing these issues (e.g., Tomasello et al. 2005).

To conclude, we thank the commentators for providing a stimulating range of perspectives on the target article, and for their numerous constructive suggestions for directions for future research. We are optimistic that pursuing these and related lines of work, across disciplines as diverse as linguistics, primatology, developmental psychology, and neurobiology, may help construct a new synthesis for understanding the complex relationship between brains, genes, and language.

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NOTES

1. Although others have used the term "the logical problem of language evolution" to point to evolutionary issues relating to UG (Botha 1999; Roberts et al. 2005), we are – to the best of our knowledge – the first to use it as an overarching label for the combined theoretical issues facing both adaptationist and non-adaptationist explanations of UG.

2. Of course, differences do exist between signed and spoken languages relating to the differences in the modality and mode of transfer of information. This raises the intriguing possibility that subtle differences in language structure and use may exist due to differences in the constraints imposed on the mechanisms subserving signed and spoken languages. For example, Conway and Christiansen (2005; 2006; in press) have shown that visual and auditory sequential learning may involve separate modality-specific, but computationally similar, mechanisms, giving rise to both qualitative and quantitative differences in the processing of auditory and visual sequences. Such differences may shape signed and spoken languages in slightly different ways so as to better fit modality-specific constraints on sequential learning.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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